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A revision of the genus *Vorticella* (Ciliophora: Peritrichida)

A. Warren

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A revision of the genus *Vorticella* (Ciliophora: Peritrichida)

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Introduction

Anyone who has had experience with the identification of free-living ciliates will be familiar with the difficulty of distinguishing the species of *Vorticella*. Their plastic body shape, variable size and highly contractile nature has made them among the most difficult of ciliates to study and identify. This has resulted in the erection of numerous species and varieties many of which are of doubtful taxonomic status.

The last major revision of the genus *Vorticella* was that of Noland & Finley (1931) who found in the literature over 200 names and descriptions. Many were clearly not congeneric, the majority being either rotifers or other protozoa but even after the rejection of these, some 94 nominal species still remained. Over the intervening 50 years another 113 species and varieties have been added giving a total of 209. With so many taxa, the descriptions of which are spread throughout the literature, the task of the ecologist trying to identify individual isolates has become particularly onerous even with the aid of identification keys such as those of Stokes (1885*a*), Kahl (1935), Curds (1969), Stiller (1971) and Green (1974).

The aim of this paper is to provide both the ecologist and the specialist in peritrichs, with a functional classification of the species of *Vorticella*. For this purpose Noland & Finley (1931) have been imitated in that a checklist of the 209 named taxa has been compiled and the taxonomic status of each determined. Drawings and descriptions of the extant species of *Vorticella* are given and a key to their identification has been constructed.

Systematics

In the scheme adopted by the Committee on Systematics and Evolution of the Society of Protozoologists (Levine *et al.*, 1980), based on the classification of Corliss (1979), the taxonomic position of the genus *Vorticella* is given as follows:

Subkingdom:	Protozoa Goldfuss, 1818 emend. von Siebold, 1845
Phylum:	Ciliophora Doflein, 1901
Class:	Oligohymenophora de Puytorac *et al.*, 1974
Subclass:	Peritrichia Stein, 1859
Order:	Peritrichida Stein, 1859
Suborder:	Sessilina Kahl, 1933
Family	Vorticellidae Ehrenberg, 1838
Genus:	*Vorticella* Linnaeus, 1767

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Diagnosis

The following list of characters serve to define the genus *Vorticella*. Body borne upon a contractile stalk, always solitary although many species are gregarious. Zooids commonly inverted bell-shape but may also be spherical, cylindrical or cone-shape. Oral cilia in three rows, two inner (polykineties) and one outer (haplokinety) which wind counter-clockwise around the peristome when viewed from above. Somatic cilia absent in the normal adult cell. Each zooid contains a single macronucleus accompanied by a small, oval micronucleus. The macronucleus is typically long and sinuous. Impregnation by silver reveals a pattern of equally spaced horizontal lines which encircle the body. The stalk is oval in cross-section and contains a helically coiled contractile myoneme called the spasmoneme which causes contraction to take place in a spiral not a zig-zag manner. Asexual reproduction is by binary fission with one cell remaining attached to the stalk while the other becomes the migratory telotroch which has an extra row of cilia, the aboral ciliary wreath, near the aboral pole. Sexual reproduction is by conjugation and involves total fusion of the mobile microconjugant with the sessile macroconjugant.

Taxonomic characters

Traditionally the taxonomy of the vorticellae is based on the morphology of the living organism as revealed by light microscopical examination. The principal characters used are shown in Figure 1. In recent years special techniques such as silver impregnation, scanning and transmission electron microscopy (SEM & TEM) have been increasingly used to study pellicular and sub-pellicular structures in greater detail (Hobbs & Lang, 1964; Reid, 1967; Kawamura, 1973; Barlow & Finley, 1976*a*; Foissner, 1979; Carey & Warren, 1983). As a result the taxonomic importance of structures such as the pellicular striations, pores and tubercles has increased accordingly. Furthermore evidence is accumulating that ecological and behavioural factors such as host specificity (for epibionts), substrate preference, pseudocolony formation and telotroch swimming patterns may also be useful diagnostic characters (Nenninger, 1948; Barlow & Finley, 1976*b*; Horikami & Ishii, 1981). The most important taxonomic features are discussed below and it is recommended that as many of these as possible should be considered when describing a new isolate.

BODY SHAPE. The outline form is the first and most readily recognisable feature of the *Vorticella* zooid. Although commonly inverted bell-shape, a range of body forms occur throughout the genus including species which are spherical (*V. globularia, V. sphaerica*), cylindrical (*V. aequilata, V. elongata*) and conical (*V. kenti, V. patellina*). This variety of form introduces a problem of definition since the interpretation of body shape can be highly subjective: what is elongate to one observer can be ellipsoidal to another. Methods of quantifying body shape for more objective mathematical analyses were investigated by Roberts *et al* (1983). It should also be noted that the body contour of some species is readily changeable (e.g. *V. inconstantans*) and that nearly all vorticellae alter their shape as conditions change in a culture or in a drop under examination. In view of this only freshly isolated and healthy specimens should be used when describing body shape.

SIZE. Size is usually expressed in terms of the overall length and maximum width of the zooid. The length is measured from the scopula, i.e. the stalk–zooid junction, to the upper rim of the peristomial lip and the width is measured at the widest part of the body below the peristome. There is often considerable variability within, and overlap between the various taxa in terms of size, and dimensions are frequently given as average values within defined ranges. Kahl (1935) has suggested that size ratios, such as zooid length: zooid width or peristomial lip width: zooid width, might be a more useful method of expressing these dimensions. Clearly, taken alone size does not constitute a particularly secure criterion of species but it does serve to reinforce other more distinctive features.

COLOUR. There are three main sources of colour within the zooid; the cytoplasm, the contents of the food vacuoles and cytoplasmic inclusions. The first two were rejected by Noland & Finley

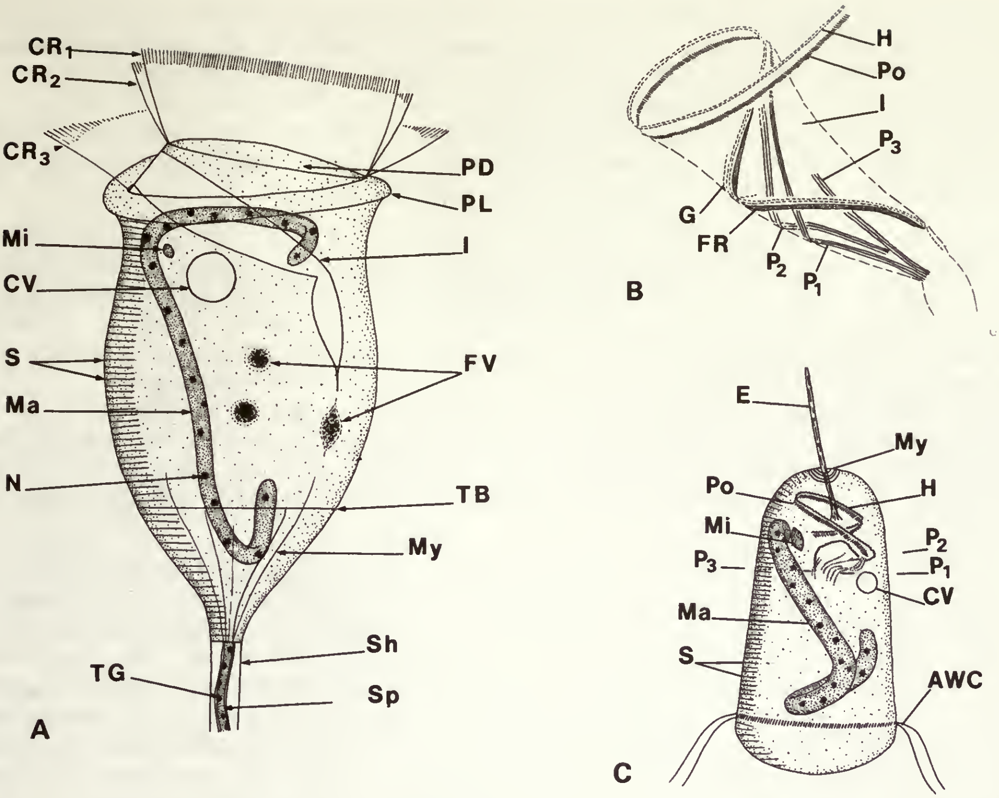

Fig. 1. A generalised *Vorticella*: (a) zooid; (b) buccal infraciliature; (c) telotroch. AWC aboral wreath of cilia; CR$_{1-3}$ 1st, 2nd & 3rd ciliary rows; CV contractile vacuole; E epistomial membrane; FR filamentous reticulum; FV food vacuole; G germinal row of kineties; H haplokinety; I infundibulum; Ma macronucleus; Mi micronucleus; My myoneme; N nucleolus; P$_{1-3}$ 1st, 2nd & 3rd peniculus; PD peristomial disc; PL peristomial lip; Po polykinety; S striations; Sh sheath; Sp spasmoneme; TB telotroch band; TG thecoplasmic granule.

(1931) as being of little taxonomic significance since both are known to vary in colour according to ecological conditions and food source respectively. The cytoplasmic inclusions consist of endosymbiotic zoochlorellae, waste and reserve granules. Noland & Finley (1931) recommended that species diagnoses should be established on grounds other than the presence of intracellular zoochlorellae pending further studies on the stability of the symbiotic relationship. Following their ultrastructural studies of two species of *Chlorella*-containing *Vorticella*, Graham & Graham (1978 & 1980) concluded that the relationship is stable and that the presence of endosymbiotic zoochlorellae may be accepted as a reliable taxonomic character.

Peristomial Lip. The peristomial lip, also referred to as the peristome border or bell margin, is the contractile rim that encompasses the anterior end of the cell. Upon contraction the lip constricts enclosing the peristomial disc and cilia which are withdrawn below. The peristomial lip usually takes the form of a simple rim but in some species, such as *V. campanula*, it projects from the periphery of the body in a shelf-like manner while in others it is ornamented by frill-like undulations (*V. cratera*), spine-like projections (*V. pulchra*) or tubercles and granules (*V. vernalis, V. verrucosa*).

The diameter, thickness and degree of eversion of the peristomial lip have a considerable influence on the overall appearance of the zooid and are commonly included in species descriptions. However, Noland & Finley (1931) highlighted the variability of these parameters with changing environmental conditions observing that 'nearly all vorticellae alter the degree of eversion and even the width of the border as conditions change in the surrounding medium'. They concluded that the variability of the lip was too great to justify placing much weight on it. Conversely, in a study of symphoriont peritrichs, Vavra (1961) found that the peristome remained constant over a range of environmental conditions. Clearly further studies on variability are required but it is generally accepted that the peristomial lip of a healthy, freshly mounted specimen constitutes a useful diagnostic feature.

PERISTOMIAL DISC. The peristomial disc (epistomial disc) is the area at the apical end of the cell encircled by the rows of cilia. In some species (e.g. *V. bivacuolata, V. elongata*) the disc is typically arched high above the peristome whilst in others it is flattened or only slightly elevated. It has been reported that most species react to unfavourable conditions by becoming increasingly globular and developing a protruding disc (Noland & Finley, 1931). Therefore the shape of the peristomial disc should only be described for healthy, freshly mounted specimens.

Silver staining reveals the presence on the disc of concentric rings of silver lines similar to those found on the rest of the zooid (Klein, 1926 & 1927) although these have not been studied in detail. Ridges or undulations radiating from the centre to the periphery and pellicular secretions may also be present but these are considered to be transitory features of little taxonomic value (Noland & Finley, 1931).

MACRONUCLEUS. *Vorticella* has a single macronucleus which is typically long and sinuous. The shape and position within the zooid of the macronucleus are useful diagnostic features although variation throughout the genus is limited. The two conformations most commonly found are J- and C-shaped. The J-shaped macronucleus lies longitudinally with respect to the major axis of the zooid, its upper arm curved horizontally across the peristome and its distal end bent upwards (Fig. 1). The C- or horse shoe-shaped macronucleus is often shorter and is usually situated in the central or anterior part of the zooid. Its orientation may be either longitudinal (e.g. *V. longifilum, V. pulchra*) or horizontal (e.g. *V. striata, V. communis*) with respect to the major axis of the zooid. The length and degree of curvature of the C-shaped macronucleus vary considerably from short and only slightly curved (e.g. *V. exilis*) to highly elongate and curved in a ring-like manner (e.g. *V. operculariformis*). Some vorticellae have macronuclei which are irregular in shape (e.g. *V. muralis, V. nutans*) while in others (e.g. *V. macrophya, V. quadrangularis*) the macronucleus has yet to be described.

Macronuclei are readily demonstrated using standard nuclear stains such as the Feulgen Reaction (Mackinnon & Hawes, 1961) and methyl green (Curds *et al*, 1983). The macronucleus is usually accompanied by a small, oval micronucleus. The micronucleus shows little variety among the different species and is difficult to observe in the living animal. Therefore it is not considered to be a particularly useful diagnostic feature.

BUCCAL APPARATUS AND CILIATURE (Fig. 1b). Infraciliary buccal patterns, which have been extensively studied in most ciliate groups and often with far reaching taxonomic consequences, have received comparatively little attention among the peritrichs. A notable exception was the exhaustive study carried out by Lom (1964) and it is from this work that much of our current knowledge is derived.

The ciliature of the adult *Vorticella* zooid is confined to the anterior end of the cell. It consists of three rows of cilia, two inner rows or polykineties (PO) and one outer row or haplokinety (H). These are situated around the edge of the peristomial disc where they perform a $1–1\frac{1}{2}$ turn of the peristome before plunging down into the infundibulum. Here the two separate, the PO passing directly downwards whereas the H follows the border of the infundibulum before sinking downwards. The PO and H are now 180° out of phase as they continue their counter-clockwise spiral down the funnel-shape infundibulum (Fig. 1b). At the base of the infundibulum is the cytostome which leads to the cytopharynx. The cytopharynx is a non-ciliated tube-like structure not usually visible in the living animal although its length and position can be ascertained by watching food vacuoles pass through. The overall length and orientation within the cell of the infundibulum and cytopharynx are often included in species diagnoses. However, Lom (1964)

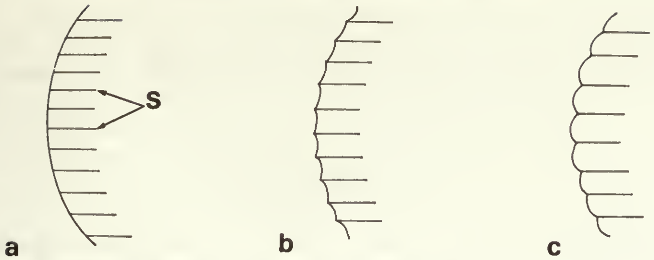

Fig. 2. The three types of ribbing between the striations (S) on the pellicle of *Vorticella*: (a) normal; (b) concave; (c) convex (b & c, after Foissner & Schiffmann, 1974).

concluded that the uniformity of peritrich buccal structures limits their use in the differentiation of closely related species.

Contractile vacuole (C.V.). Most vorticellae have a single c.v. and this is usually situated just beneath the peristome, close to the infundibulum. In some species a second c.v. is present and this is also located in the anterior part of the cell usually on the opposite side of the infundibulum to the first c.v. Thus while the position of the c.v.(s) is comparatively uniform throughout the genus, the number of c.v's per zooid is a useful diagnostic feature. It has also been suggested that the diameter and rate of pulsation of the c.v. may be valuable aids for distinguishing species (Noland & Finley, 1931). However these parameters should only be considered in the light of the osmotic conditions of the surrounding medium.

Pellicle. The structure of the pellicle of *Vorticella* corresponds closely with that of other ciliates. It consists of a single plasma membrane overlaying a system of membrane-bound alveolar sacs which in turn lie between transversely orientated pellicular ridges (Kawamura, 1973). In many species these ridges are well developed and are clearly visible under the light microscope as transverse striations encircling the body. These striations, along with the pellicular pores which are also found all over the zooid surface, have become increasingly important in peritrich taxonomy in recent years. Special techniques such as silver staining and SEM have been employed to study pellicular structures in detail (Hobbs & Lang, 1964; Small & Ranganathan, 1970; Davidson & Finley, 1972; Barlow & Finley, 1976*a* & *b*; Carey & Warren, 1983). The distribution patterns formed by the pores and striations have been analysed biometrically (Reid, 1967; Foissner & Schiffmann, 1974 & 1975; Foissner, 1979 & 1981).

Further variations in the pellicle occur in those areas between the striations. For the majority of vorticellae the pellicle in these areas follows the contour of the zooid when the animal is viewed in profile. However in some species the pellicle curves inwards while in others it bulges out (Fig. 2). Foissner & Schiffmann (1974) referred to these two pellicle types as concave and convex respectively. The configuration of the pellicle between the striations, or 'ribbing', is determined by the shape of the underlying alveolar sacs.

Other pellicular structures which are rather less common and are found in relatively few species include tubercles (e.g. *V. perlata*), spines (*V. voeltzkowi*), mucus layers (*V. rhabdophora*) and membranous sacs (*V. vestita*). Although the functions of these structures are generally not known, they are useful characters for recognising species.

Stalk. The stalk is probably the most characteristic structure of *Vorticella*. A comprehensive study of its ultrastructure was made by Randall & Hopkins (1962) but basically it consists of an outer wall or sheath enclosing a fibrillar matrix which supports a contractile cord. The cord consists of a membrane-bound layer of cytoplasm, or 'thecoplasm', and placed excentrically within this is the contractile myoneme or 'spasmoneme'. The thecoplasm often contains numerous small refractile bodies called thecoplasmic granules which lie alongside the spasmoneme in longitudinally arranged spiral rows. When present, these granules are usually colourless but in two species (*V. picta* and *V. rubristigma*) they are coloured either green or red. The function of the thecoplasmic granules is not known and in several species they are absent altogether.

Stalk length has long been used as a diagnostic feature for species of *Vorticella*. However although stalk length does tend towards a modal value in many species, individual variation is too great to justify much taxonomic reliance. Other parameters which appear to be more consistently uniform are stalk width and the length of one complete turn of the spasmoneme spiral, i.e. the internode distance. Noland & Finley (1931) found a direct mathematical relationship between the two, the internode distance being approximately ten times the stalk width.

The stalk sheath shows some variability within the genus. For most vorticelliae the sheath is untwisted when the stalk is fully extended but in a few species (e.g. *V. flexuosa* and *V. gracilis*) it is twisted and in some cases has an even greater spiral curvature than the contained spasmoneme. Occasionally the sheath may also have distinct rings or annulations (e.g. *V. annulata*). According to Noland & Finley (1931) these annuli represent points of cell division and are transitory features of little taxonomic value.

TELOTROCHS. The telotroch is the free-swimming stage of the *Vorticella* life cycle and is formed as a result of asexual reproduction (binary fission). Telotrochs are usually cylindrical or cone-shape and possess an extra row of cilia, the aboral ciliary wreath, near the scopular region (Fig. 1c). They swim with the aboral end facing forwards and the peristome, which remains closed, facing backwards.

Although studied in relatively few species, telotrochs exhibit several potentially useful taxonomic characters, both morphological and behavioural. Morphological features of diagnostic value include size, shape and pellicular structures. Telotroch behaviour is even less well documented than morphology, a notable exception being Barlow & Finley's (1976*b*) study of swimming patterns and settling activities of four *Vorticella* spp. It was noted that each of the four species had its own characteristic behaviour pattern.

It has long been known that certain species of *Vorticella* form pseudocolonies while others remain solitary (Kent, 1880–1882; Spoon, 1974). Horikami & Ishii (1981) reported that the adult zooids of pseudocolony-forming species such as *V. convallaria, V. campanula* and *V. vestita* secrete a transparent viscous compound which acts as an attractant to the telotrochs. As a result of this positive chemotactic response the telotrochs settle on the substrate close to the attached adult cells.

CYSTS. Cysts and the processes of encystation and excystation have been described in detail for only one species, *V. microstoma* (Brand, 1923; Finley & Lewis, 1960). The presence of cysts has been reported in few other species. Although Corliss & Esser (1974) have highlighted the importance of cysts in peritrich ecology, our knowledge of the *Vorticella* cyst is meagre and its taxonomic application has yet to be explored.

ECOLOGICAL FACTORS. It has long been recognised that different species of *Vorticella* often have a predilection for different ecological conditions (Kolkwitz & Marsson, 1909; Noland, 1925). Various physico–chemical and biological factors have been identified as being of primary importance in determining the distribution of peritrichs. These include the concentration of organic pollution (BOD); food source; flow rate; substrate preference, and relationships with predators and parasites.

The ability of different species of *Vorticella* to tolerate different levels of organic pollution was used by Kolkwitz & Marsson (1909) to form the basis of the first saprobic system for measuring water quality. Originally four saprobic zones were designated according to the species of *Vorticella* which predominate in each. More recently Sládećek (1971) defined the saprobic sequence of thirty-two species of *Vorticella*.

Of the other ecological factors food source (Curds & Vandyke, 1966), flow rate (Zimmerman, 1961), substrate preference (Sládečková, 1962) and relationships with predators and parasites (Noland, 1925; Spoon, 1975) may all provide useful information to aid species diagnoses although in most cases these have yet to be studied in sufficient detail. Taken alone these factors would be a very insecure criteria of species but they may serve to reinforce other more distinctive features.

Key to Species

Eighty-two species of *Vorticella* are recognised and may be identified with the aid of the following key. The morphological and behavioural characters used refer to those observed in healthy, freshly mounted specimens.

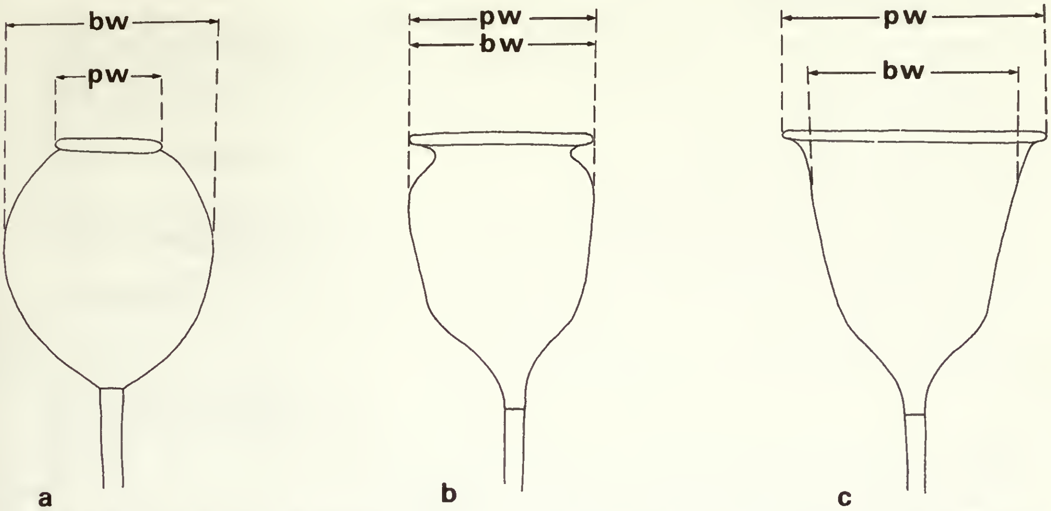

Fig. 3. Size of peristomial lip (PL) in relation to greatest body width (BW): (a) PL$<$BW; (b) PL$=$BW; (c) PL$>$BW.

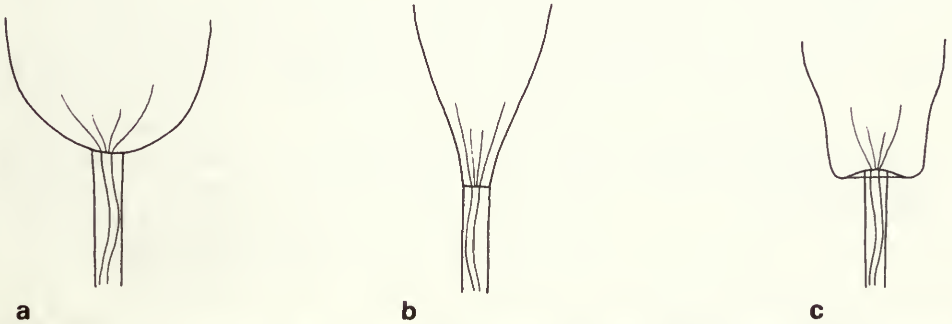

Fig. 4. Shape of scopular region of zooid: (a) rounded; (b) tapering; (c) truncated and overlapping.

1	Pellicle striated	2
–	Pellicle unstriated	61
2	Free-swimming and never attached to a substratum	3
–	Sessile, attached to substratum by its stalk	4
3	When swimming, stalk is held projecting forwards	***V. natans*** (Fig. 32c)
–	When swimming, stalk is used as a giant whip-like flagellum	***V. mayeri*** (Fig. 30)
4	Zooid does not contain endosymbiotic zoochlorellae.	5
–	Zooid contains endosymbiotic zoochlorellae	***V. chlorostigma*** (Fig. 12b)
5	Spasmoneme has red or green thecoplasmic granules.	6
–	When present, thecoplasmic granules are colourless	7

6 Zooid small, approximately 20 µm long × 10 µm wide, with a single c.v. and red thecoplasmic granules . . . ***V. microscopica*** (Fig. 29b)
– Zooid approximately 58 µm long × 32 µm wide and with 2 c.v.'s; thecoplasmic granules red or green . . . ***V. picta*** (Fig. 36a)

7 Zooid very long measuring 170–200 µm in length . . . 8
– Zooid less than 170 µm long . . . 9

8 Zooid elongate, cylindrical in shape and with two constrictions one centrally located and one beneath the peristome . . . ***V. quadrangularis*** (Fig. 39b)
– Zooid trumpet-shaped, not constricted beneath the peristome and without a centrally located constriction . . . ***V. kenti*** (Fig. 22b)

9 Stalk less than × 10 zooid length . . . 10
– Stalk length × 10– × 20 zooid length . . . ***V. macrostyla*** (Fig. 28a)

10 Zooid without ridges; contraction normal . . . 11
– Two distinct ridges are present on lower half of zooid; upon contraction the area of zooid around each overlaps that below (see Fig. 44b) . . . ***V. telescopoides*** (Fig. 44c)

11 Macronucleus lies horizontal with respect to major body axis and is usually C-shape . . . 12
– Macronucleus lies longitudinally with respect to major body axis and is J-, C-, or irregular in shape . . . 34

12 Upon contraction, peristomial lip folds inwards . . . 13
– Upon contraction, peristomial lip is drawn up in the form of a narrow cylinder . . . ***V. lymnaearum*** (Fig. 27a)

13 Pellicle has convex ribbing between striations (see Fig. 2) . . . 14
– Pellicle has normal or concave ribbing between striations (Fig. 2) . . . 20

14 Diameter of peristomial lip less than maximum body width (see Fig. 3) . . . 15
– Diameter of peristomial lip equal to or greater than maximum body width . . . 16

15 C.V. centrally located in zooid; infundibulum reaches $\frac{3}{4}$ zooid length . . . ***V. pulchella*** (Fig. 38a)
– C.V. situated just below peristome; infundibulum reaches one-third zooid length . . . ***V. striata*** (Fig. 42a & b)

16 Zooid constricted beneath peristomial lip; pellicle has fine, narrow striations . . . 17
– Zooid not constricted beneath peristomial lip; pellicle has distinct, broadly spaced striations . . . 19

17 Disc flat and slightly elevated above peristomial lip which is not significantly thickened . . . 18
– Disc prominently arched and elevated high above peristomial lip which is significantly thickened . . . ***V. incisa*** (Fig. 21a)

18 Diameter of peristomial lip equal to maximum body width . . . ***V. marina*** (Fig. 29a)
– Diameter of peristomial lip greater than maximum body width . . . ***V. longiseta*** (Fig. 25b)

19 Zooid elongate, almost cylindrical in shape; diameter of peristomial lip equal to maximum body width (see Fig. 3) . . . ***V. macrophya*** (Fig. 27b)
– Zooid trumpet-shaped; diameter of peristomial lip greater than maximum body width . . . ***V. bidulphae*** (Fig. 9a)

20 Pellicle has concave ribbing between striations . . . 21
– Pellicle has normal ribbing between striations (Fig. 2) . . . 26

21 Diameter of peristomial lip equal to maximum body width . . . 22
– Diameter of peristomial lip less than maximum body width . . . 23

22 Stalk sheath twisted . . . ***V. limnetis*** (Fig. 24b)
– Stalk sheath not twisted . . . ***V. platysoma*** (Fig. 36b)

23 Macronucleus curved less than 360° . . . 24
– Macronucleus curved more than 360° in a ring-like manner . . . ***V. operculariformis*** (Fig. 34a)

24 Pellicular pores sparse, usually 15 or 16 per 100 µm^2 on zooid surface . . . 25
– Pellicular pores numerous with 70–120 (mean 104) per 100 µm^2 on zooid surface . . . ***V. astyliformis*** (Fig. 8a & b)

25 Zooid has total of 18–30 (mean 21) striations on pellicle . . . ***V. costata*** (Fig. 14a & b)
– Zooid has total of 34–51 (mean 42) striations on pellicle . . . ***V. infusionum*** (Fig. 21b & c)

26 Zooid has one c.v. . . . 27
– Zooid has two c.v.'s . . . ***V. dimorpha*** (Fig. 14c)

27 Diameter of peristomial lip less than × 2 maximum body width . . . 28
– Diameter of peristomial lip at least × 2 maximum body width . . . ***V. marginata*** (Fig. 28b)

28 Scopular region of zooid rounded or tapering but peripheral areas do not overlap stalk (Fig. 4a & b) . . . 29
– Scopular region of zooid not rounded or tapering; peripheral areas overlap stalk (Fig. 4c) . . . ***V. latifunda*** (Fig. 23a)

29 Diameter of peristomial lip less than maximum body width . . . 30
– Diameter of peristomial lip equal to or greater than maximum body width . . . 31

30 Zooid 60–70 µm long; stalk × 3– × 5 zooid length . . . ***V. turgicula*** (Fig. 45a)
– Zooid 25–40 µm long; stalk less than ½ zooid length . . . ***V. bosminae*** (Fig. 10a)

31 Zooid held vertically on stalk and not noticeably curved . . . 32
– Zooid curved and held at an angle to stalk . . . ***V. hamata*** (Fig. 20b)

32 Zooid elongate, length approximately × 2– × 3 maximum body width . . . 33
– Zooid inverted bell-shaped; length approximately equal to maximum body width . . . ***V. campanulata*** (Fig. 12a)

33 Zooid approximately 90 µm long; an oblique ridge is present on lower one-third of body . . . ***V. fromenteli*** (Fig. 17a)
– Zooid approximately 40 µm long and without an oblique ridge . . . ***V. parasita*** (Fig. 35a)

34 Macronucleus C-shaped . . . 35
– Macronucleus irregular or J-shaped . . . 48

35 Pellicle has convex ribbing between striations . . . 36
– Pellicle has normal or concave ribbing . . . 37

36 Upon contraction, peristomial lip becomes puckered (see Fig. 43b) ***V. szczepanowskii*** (Fig. 43c)
– Upon contraction, peristomial lip is drawn up in the shape of a narrow cylinder . . . ***V. venusta*** (Fig. 45b & c)

37 Tubercles or granules present on pellicle . . . 38
– Pellicle without tubercles or granules . . . 39

38 Zooid has two c.v.'s . . . ***V. vernalis*** (Fig. 46a)
– Zooid has one c.v. . . . ***V. granulata*** (Fig. 19c)

39 Pellicle has concave ribbing between striations . . . 40
– Pellicle has normal ribbing . . . 42

40 Zooid held erect on stalk . . . 41
– Zooid held at an angle with respect to stalk . . . ***V. lima*** (Fig. 24a)

41 Zooid has a total of 38–70 (mean 58) pellicular striations . . . ***V. aequilata*** (Fig. 5a)
– Zooid has 65–89 (mean 72) pellicular striations . . . ***V. alpestris*** (Fig. 6a & b)

42 Diameter of peristomial lip less than maximum body width . . . 43
– Diameter of peristomial lip greater than or equal to maximum body width . . . 44

43 Disc prominently arched above peristome; stalk has constriction ½ way down below which it is non-contractile . . . ***V. lichenicola*** (Fig. 23b)
– Disc flat or slightly convex; stalk without constriction and contracts normally . . . ***V. microstoma*** (Fig. 31)

44 Zooid held erect on stalk . . . 45
– Zooid curved and held at an angle with respect to stalk . . . ***V. subprocumbens*** (Fig. 42c)

45 Macronucleus short, length approximately × 5 width . . . 46
– Macronucleus elongate, length greater than × 5 width . . . 47

46 Diameter of peristomial lip equal to maximum body width . . . ***V. exilis*** (Fig. 16a)
– Diameter of peristomial lip greater than maximum body width . . . ***V. longitricha*** (Fig. 26a)

47 Peristomial lip has several spine-like projections; stalk sheath not twisted . ***V. pulchra*** (Fig. 38b)
– Peristomial lip without spine-like projections; stalk sheath twisted . ***V. flexuosa*** (Fig. 16b & c)

48 Macronucleus irregular in shape; proximal region lies longitudinally with respect to major axis of zooid . . . 49
– Macronucleus J-shaped; proximal region lies horizontally across peristome . . . 50

49 Zooid elongate with prominent bulge in lower one-third; diameter of peristomial lip less than maximum body width . . . ***V. muralis*** (Fig. 32a & b)
– Zooid inverted bell-shaped; diameter of peristomial lip equal to or greater than maximum body width . . . ***V. jaerae*** (Fig. 22a)

50 Upon contraction buccal cilia are withdrawn into peristome which closes completely . . . 51
– Upon contraction cilia are not withdrawn and peristome only partially closes . . . ***V. elongata*** (Fig. 15b & c)

51 Pellicle has convex ribbing between striations . . . 52
– Pellicle has normal or concave ribbing . . . 53

52 Zooid has two c.v.'s . . . ***V. halophila*** (Fig. 20a)
– Zooid has one c.v. . . . ***V. lutea*** (Fig. 26b)

53 Zooid with either a membranous or mucilagenous covering . . . 54
– Zooid without a membranous or mucilagenous covering . . . 55

54 Zooid with membranous, alveolar investment . . . ***V. vestita*** (Fig. 47a)
– Zooid with mucilagenous covering . . . ***V. rhabdophora*** (Fig. 40a)

55 Diameter of peristomial lip greater than zooid length . . . 56
– Diameter of peristomial lip less than zooid length . . . 57

56 Peristomial lip with undulating, frill-like rim; cytoplasm without dark, refractile inclusions . . . ***V. cratera*** (Fig. 15a)
– Peristomial lip without frill-like rim; cytoplasm contains numerous dark, refractile inclusions . . . ***V. campanula*** (Fig. 11)

57 Pellicle has concave ribbing between striations . . . 58
– Pellicle has normal ribbing between striations . . . 59

58 Diameter of peristomial lip less than maximum body width . . . ***V. sepulcreti*** (Fig. 41b)
– Diameter of peristomial lip equal to or greater than maximum body width . . . ***V. gracilis*** (Fig. 19a & b)

59 C.V. situated in upper one-third of zooid . . . 60
– C.V. centrally located in zooid . . . ***V. banatica*** (Fig. 8c)

60 Diameter of peristomial lip less than or equal to maximum body width; zooid elongate . . . ***V. calciformis*** (Fig. 10b)
– Diameter of peristomial lip greater than maximum body width; zooid inverted bell-shaped . . . ***V. convallaria*** (Fig. 13b & c)

61 Diameter of peristomial lip less than maximum body width . . . 62
– Diameter of peristomial lip equal to or greater than maximum body width . . . 67

62 Pellicle without spine-like projections . . . 63
– Pellicle with numerous spine-like projections . . . ***V. voeltzkowi*** (Fig. 47b)

63 Zooid almost spherical in shape, body length about equal to maximum body width . . . 64
– Zooid not spherical; body length greater than maximum body width . . . 65

64 Stalk with one or more distinct annulations; usually solitary and not forming pseudocolonies . . . ***V. anomala*** (Fig. 7a)
– Stalk without annulations; typically forms pseudocolonies . . . ***V. globularia*** (Fig. 18b)

65 Zooid with one c.v. . . . 66
– Zooid with two c.v.'s . . . ***V. bivacuolata*** (Fig. 9b)

66 Diameter of peristomial lip usually greater than $\frac{1}{2}$ maximum body width; stalk length about equal to length of zooid . . . ***V. ovum*** (Fig. 34b)
– Diameter of peristomial lip about $\frac{1}{2}$ maximum body width; stalk up to ×4–×5 zooid length . . . ***V. globosa*** (Fig. 18a)

67 Stalk without annulations . . . 68
– Stalk with 1–3 distinct annulations . . . ***V. annulata*** (Fig. 6c)

68 Zooid without extracellular membranous investment . . . 69
– Zooid with extracellular membranous investment . . . ***V. aperta*** (Fig. 7b)

69 Pellicle without tubercles . . . 70
– Pellicle with numerous irregular tubercles . . . ***V. verrucosa*** (Fig. 46b)

70 Zooid without a distinct ridge in region of telotroch band . . . 71
– Zooid with a distinct ridge in region of telotroch band . . . ***V. obconica*** (Fig. 33b)

71 Macronucleus lies horizontal with respect to major axis of zooid 72
– Macronucleus lies vertical with respect to major axis of zooid 74
72 Scopular region of zooid tapers towards stalk (see Fig. 4) 73
– Scopular region of zooid rounded and does not taper towards stalk . ***V. communis*** (Fig. 13a)
73 Diameter of peristomial lip greater than maximum body width . . ***V. pyriforme*** (Fig. 39a)
– Diameter of peristomial lip less than or equal to maximum body width . ***V. rotunda*** (Fig. 40b)
74 Macronucleus J-shaped 75
– Macronucleus straight, irregular or C-shaped 77
75 When present, thecoplasmic granules colourless 76
– Thecoplasmic granules red . . . . ***V. rubristigma*** (Fig. 41a)
76 Zooid 68–85 µm long; macronucleus typically long and thin . . ***V. poznaniensis*** (Fig .37)
– Zooid 88–100 µm long; width of macronucleus normal . . . . ***V. fusca*** (Fig. 17b)
77 Zooid without distinct pellicular ridges; contraction normal 80
– Two parallel transverse ridges are present on lower $\frac{1}{2}$ of zooid; upon contraction, the area of zooid above each overlaps that below (see Fig. 44b) . . . ***V. telescopica*** (Fig. 44a)
78 Diameter of peristomial lip less than zooid length 79
– Diameter of peristomial lip equal to or greater than zooid length . ***V. patellina*** (Fig. 35b)
79 Zooid held in vertical position with respect to stalk 80
– Zooid held in characteristic nodding position . . . . ***V. nutans*** (Fig. 33a)
80 Macronucleus short, length approximately ×5–×6 width, and slightly curved; stalk less than ×5 zooid length 81
– Macronucleus elongate, length approximately ×15 width, with both ends sharply curved; stalk approximately ×10 zooid length . . . . ***V. longifilum*** (Fig. 25a)
81 Disc prominently arched above peristome; infundibulum reaches two-thirds zooid length . . . . ***V. subsinuata*** (Fig. 43a)
– Disc flat; infundibulum short, terminating in upper one-third of zooid . ***V. alba*** (Fig. 5b)

Species descriptions

The recognised species with their synonyms are given below.

V. aequilata Kahl, 1939

DIAGNOSIS (Fig. 5a): zooid 40–50 µm long × 20 µm wide, peristomial lip 15 µm in diameter; peristomial region constricted giving zooid the appearance of a somewhat elongated barrel; peristomial disc bulges prominently above lip; pellicle clearly striated; macronucleus C-shaped and situated longitudinally along the axis of the body; one c.v. situated near the cytopharynx; stalk up to 200 µm long.

HABITAT. Freshwater and marine.

REMARKS. For biometric analysis see Reid (1967).

V. alba Fromentel, 1874

DIAGNOSIS (Fig. 5b). Zooid 60–80 µm long × 25 µm wide, inverted bell-shaped and constricted below peristomial lip which measures 25 µm across; disc convex; infundibulum reaches one-third body length; C.V. situated in upper one-third of zooid; macronucleus C-shaped and lies longitudinally in centre of body; pellicular striations not visible; stalk 180–300 µm long.

HABITAT. Freshwater, solitary.

V. alpestris Foissner, 1979

DIAGNOSIS (Figs 6a & b). Zooid 35–45 µm long × 20 µm wide; body constricted beneath peristomial lip which measures 20 µm across; infundibulum nearly reaches centre of zooid; C.V. lies just above centre of body and empties into ventral wall of infundibulum; macronucleus J-shaped and situated longitudinally with respect to major axis of zooid; pellicle distinctly striated with concave ribbing between striations.

HABITAT. Freshwater.

REMARKS: Foissner's (1979) original description includes a biometric analysis.

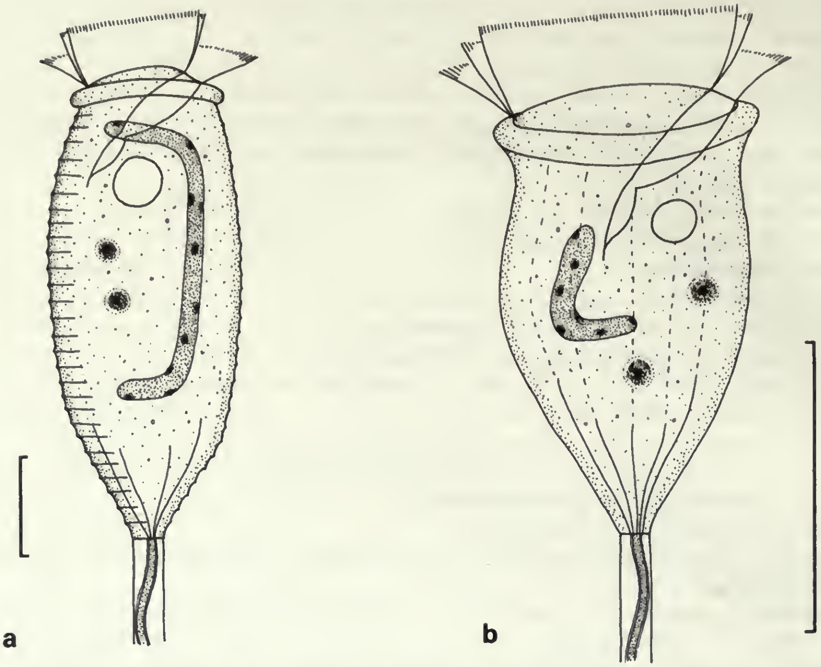

Fig. 5. (a) *V. aequilata* (after Kahl, 1935) bar = 10 µm; (b) *V. alba* (after Curds, 1969), bar = 50 µm.

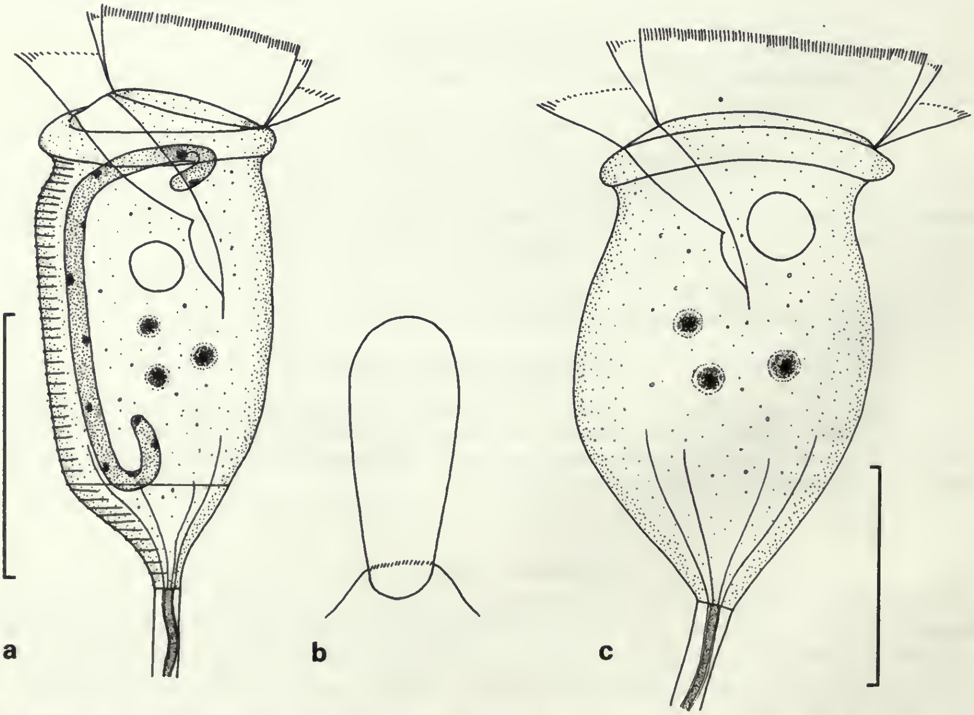

Fig. 6. (a) *V. alpestris* zooid, bar = 25 µm; (b) telotroch (after Foissner, 1979), bar = 10 µm; (c) *V. annulata* (after Gourret & Roeser, 1888), bar = 25 µm.

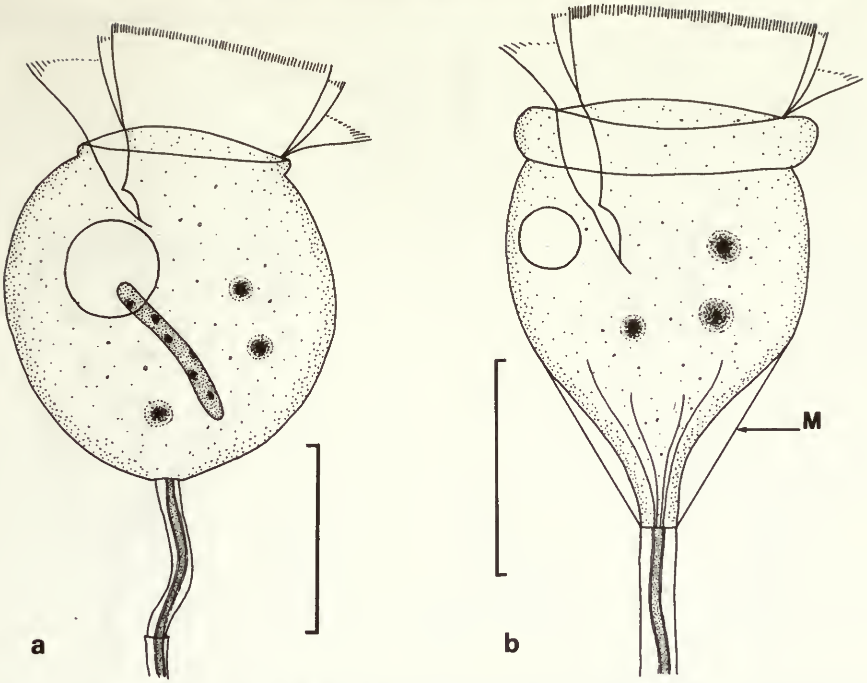

Fig. 7. (a) *V. anomala* (after Gourret & Roeser, 1886), bar = 25 μm; (b) *V. aperta* (after Fromentel, 1874), bar = 25 μm, M = membrane.

V. annulata (Gourret & Roeser, 1888) Kahl, 1935

V. brevistyla var. *annulata* Gourret & Roeser, 1888

DIAGNOSIS (Fig. 6c). Zooid 55 μm long × 35 μm wide, inverted bell-shaped with constriction beneath peristomial lip which measures 35 μm across; C.V. situated just below peristome; stalk up to 200 μm long with two or more distinct annulations.

HABITAT. Marine.

V. anomala Gourett & Roeser, 1886

DIAGNOSIS (Fig. 7a). Zooid spherical in shape, 40 μm in diameter; disc prominently arched above narrow peristomial lip; macronucleus short and straight and lies obliquely across lower part of body; C.V. centrally located; pellicular striations not visible; approximately half-way down stalk is a ridge below which the stalk is wider and non-contractile.

HABITAT. Marine, solitary

V. aperta Fromentel, 1874

DIAGNOSIS (Fig. 7b). Zooid 60 μm long × 45 μm wide, inverted bell-shaped and constricted below peristomial lip which measures 45 μm across; disc flat or slightly concave; infundibulum short; C.V. situated just below peristome; pellicular striations not visible; entire zooid covered by a smooth membranous layer which is most easily seen in lower region; stalk up to 200 μm long.

HABITAT. Freshwater.

V. astyliformis Foissner, 1981

DIAGNOSIS (Fig. 8a & b). Zooid 30–50 μm long × 35–45 μm wide, nearly spherical in shape with a narrow peristomial lip which measures 20 μm across; infundibulum reaches centre of zooid; C.V. situated just below

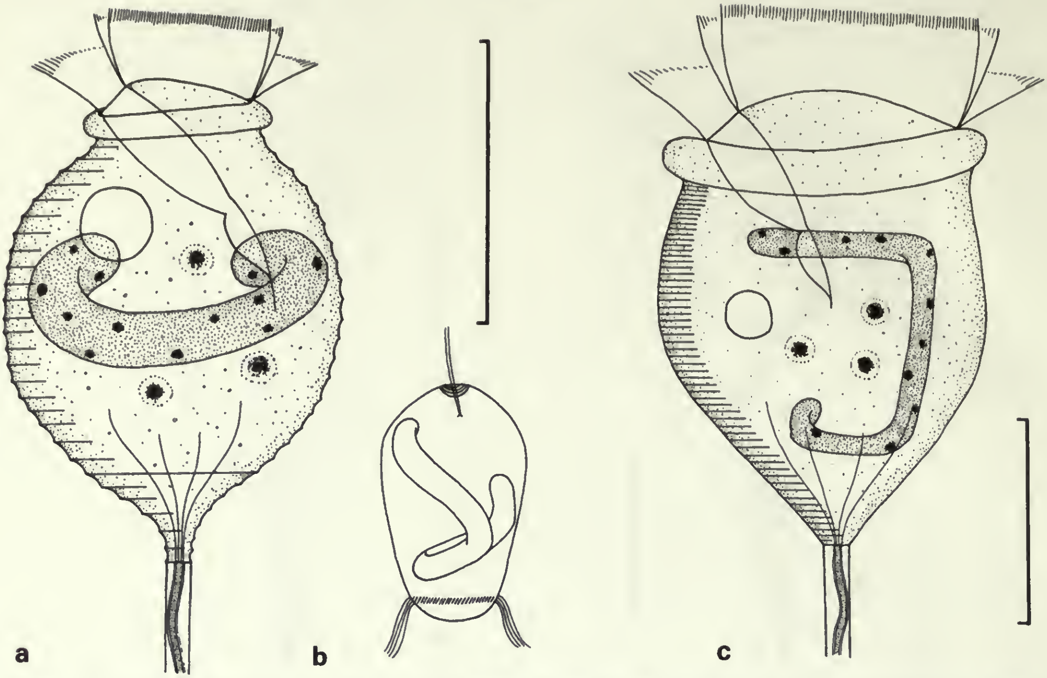

Fig. 8. (a) *V. astyliformis* zooid; (b) telotroch (after Foissner, 1981), bar = 25 µm; (c) *V. banatica* (after Stiller, 1971), bar = 25 µm

peristome and empties into left hand wall of infundibulum; macronucleus C-shaped and lies horizontal to the major axis of the zooid; pellicle clearly striated and has concave ribbing between striations; telotroch is slender with a prominent epistomial membrane.

HABITAT. Freshwater, originally isolated from Alpine soils.

V. banatica Lepsi

DIAGNOSIS (Fig. 8c). Zooid 60–80 µm long × 50 µm wide, inverted bell-shaped with a well developed peristomial lip which measures 55 µm across; disc prominently arched above peristome; infundibulum reaches one-third body length; C.V. situated just above centre of zooid; macronucleus long and J-shaped with upper arm lying across peristome; pellicle finely striated; stalk slender and up to 80 µm long.

REMARKS. Drawing and description from Stiller (1971).

V. bidulphae Stiller, 1939

V. variabilis Stiller, 1939.

DIAGNOSIS (Fig. 9a). Zooid 40 µm long × 20 µm wide, triangular in shape with a broad peristomial lip measuring 35–45 µm across; disc flat or slightly convex; infundibulum reaches centre of zooid; C.V. situated in upper one-third of body and empties into right hand wall of infundibulum via a short channel; macronucleus C-shaped and lies transversely across centre of zooid; pellicle distinctly striated with convex ribbing between the striations; stalk up to 120 µm long; cysts measure 32 µm in diameter.

HABITAT. Marine, originally isolated from the North Sea attached to *Bidulphae chinensis*.

V. bivacuolata Fukui & Morishita, 1961

DIAGNOSIS (Fig. 9b). Zooid 95–120 µm long × 55–68 µm wide, barrel-shaped and constricted below well developed peristomial lip which measures 60 µm across; disc prominently arched above peristome;

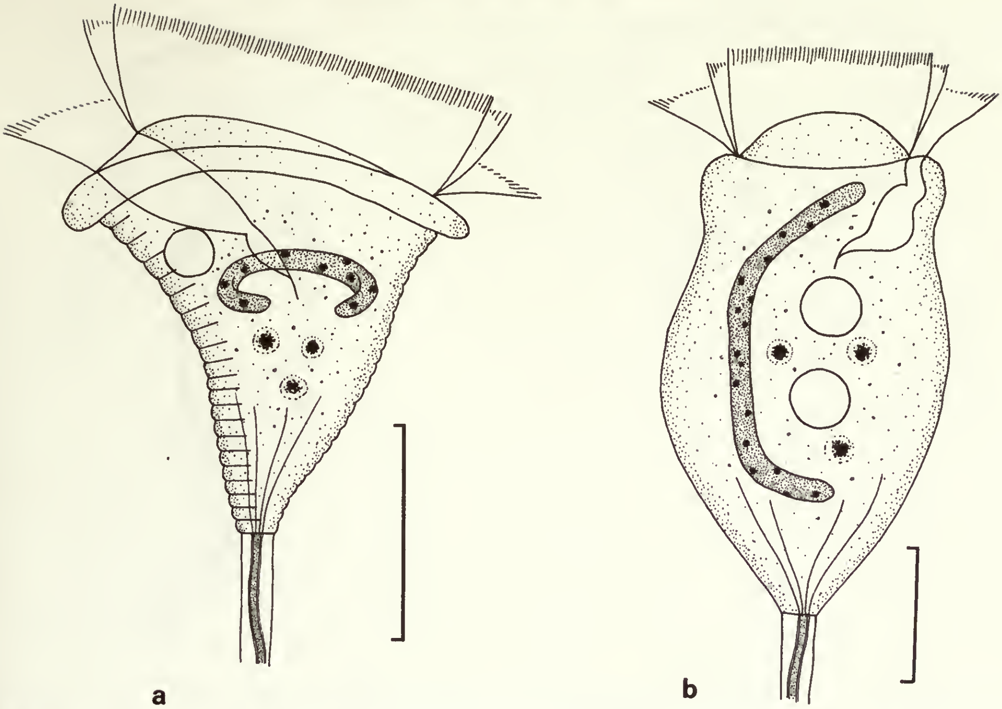

Fig. 9. (a) *V. bidulphae* (after Stiller, 1939), bar = 25 µm; (b) *V. bivacuolata* (after Fukui & Morishita, 1961), bar = 25 µm.

infundibulum short; two C.V.'s centrally located in body; macronucleus long, C-shaped and lies longitudinally with respect to major axis of body; pellicular striations not visible; stalk 3·0–4·0 µm wide.

Habitat. Freshwater, originally isolated from activated sludge.

V. bosminae Šramek-Hušek, 1948

Diagnosis (Fig. 10a). Zooid 25–40 µm long × 20–30 µm wide, somewhat rotund and constricted below peristomial lip which measures 15–20 µm across; C.V. situated just below peristome; macronucleus C-shaped and lies transversely across centre of body; pellicle distinctly striated; stalk up to 20 µm long.

Habitat. Freshwater, originally isolated from pond water as an epizooite attached to the crustaceans, *Bosmina longirostris, Thermocyclopsis hyalinus, Mesocyclopsis leukarti* and *M. viridis.*

V. calciformis Kahl, 1933

Diagnosis (Fig. 10b). Zooid 90 µm long × 65 µm wide, constricted below peristomial lip which measures 65 µm across; disc flat and obliquely elevated above peristome; C.V. small and situated just below peristome; macronucleus long and J-shaped lying longitudinally with respect to major axis of body; pellicle distinctly striated.

Habitat. Marine

V. campanula Ehrenberg, 1831

V. campanula f. *minor* Stiller, 1953
V. campanula f. *citrina* var. *minor* Stiller, 1953
V. cylindrica Dons, 1915
V. dilatata (Fromentel, 1874), Noland & Finley, 1931
V. lunaris (Muller, 1773) Noland & Finley, 1931

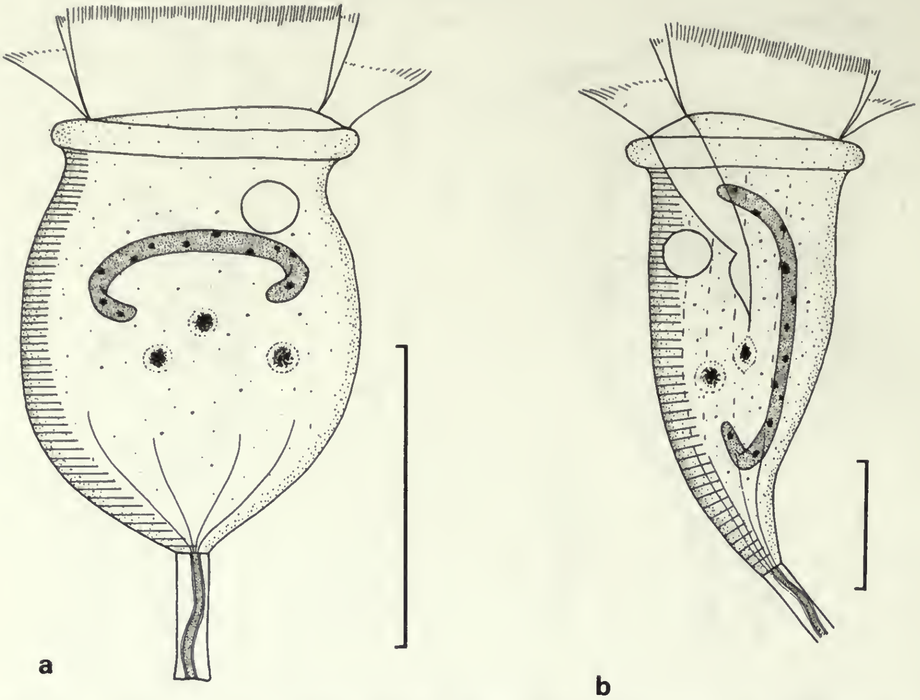

Fig. 10. (a) *V. bosminae* (after Šramek-Hušek, 1948), bar = 25 µm; (b) *V. calciformis* (after Kahl, 1935), bar = 25 µm.

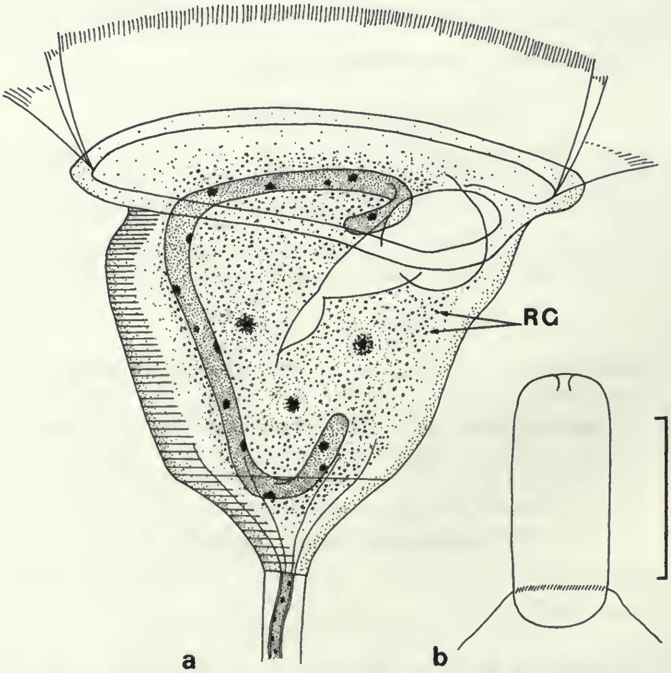

Fig. 11. *V. campanula* (a) zooid; (b) telotroch (after Noland & Finley, 1931), bar = 25 µm.

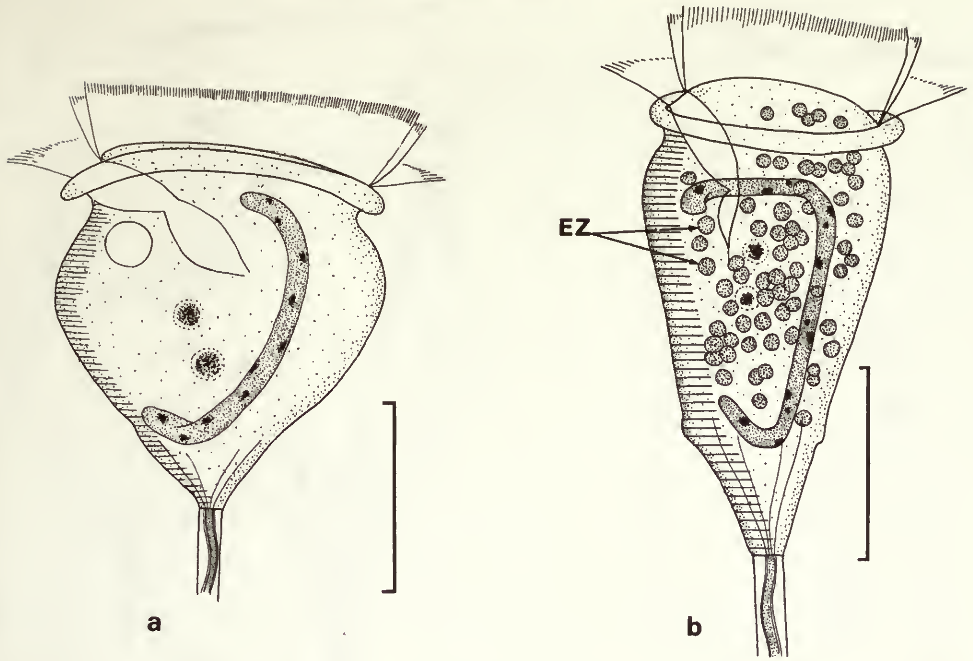

Fig. 12. (a) *V. campanulata* (after Šramek-Hušek, 1948), bar = 25 µm; (b) *V. chlorostigma* (after Stiller, 1941), bar = 25 µm.

V. macrostoma Schmarda, 1854
V. margaritifera (Fromentel, 1874) Noland & Finley, 1931
V. patellina (Ehrenberg, 1831) Noland & Finley, 1931

Diagnosis (Figs 11a & b). Zooid 50–157 µm long (mean 68 µm) × 35–99 µm wide (mean 58 µm); inverted bell-shaped and constricted below peristomial lip which measures 60–125 µm across (mean 78 µm); upon contraction, peristomial lip becomes puckered; disc flat and obliquely elevated above peristome; infundibulum broad; C.V. situated in upper one-third of zooid; macronucleus long, J-shaped and situated longitudinally in body with upper arm lying horizontally across peristome; cytoplasm contains numerous dark, refractile granules; pellicle finely striated; stalk up to 500 µm long and spasmoneme has numerous thecoplasmic granules.

Habitat. Freshwater or marine; often forms large pseudocolonies; occasionally epibiotic on various aquatic arthropods (Green, 1974).

Remarks. For biometric analysis, see Foissner & Schiffmann (1974).

V. campanulata (Kahl, 1933) Šramek-Hušek, 1948

V. constricta Kahl, 1933

Diagnosis (Fig. 12a). Zooid 45 µm long × 50 µm wide and constricted beneath peristomial lip which measures 50 µm across; disc flat; infundibulum reaches one-third zooid length; c.v. situated just beneath peristome; macronucleus C-shaped and situated longitudinally in zooid; pellicle striated.

Habitat. Freshwater or marine.

Remarks. Šramek-Hušek (1948*b*) isolated a vorticellid from the River Vltave, Prague which he identified as *V. constricta* Kahl, 1933. It was renamed *V. campanulata* in order to solve the problem of homonymy with Fromentel's (1874) *V. constricta*.

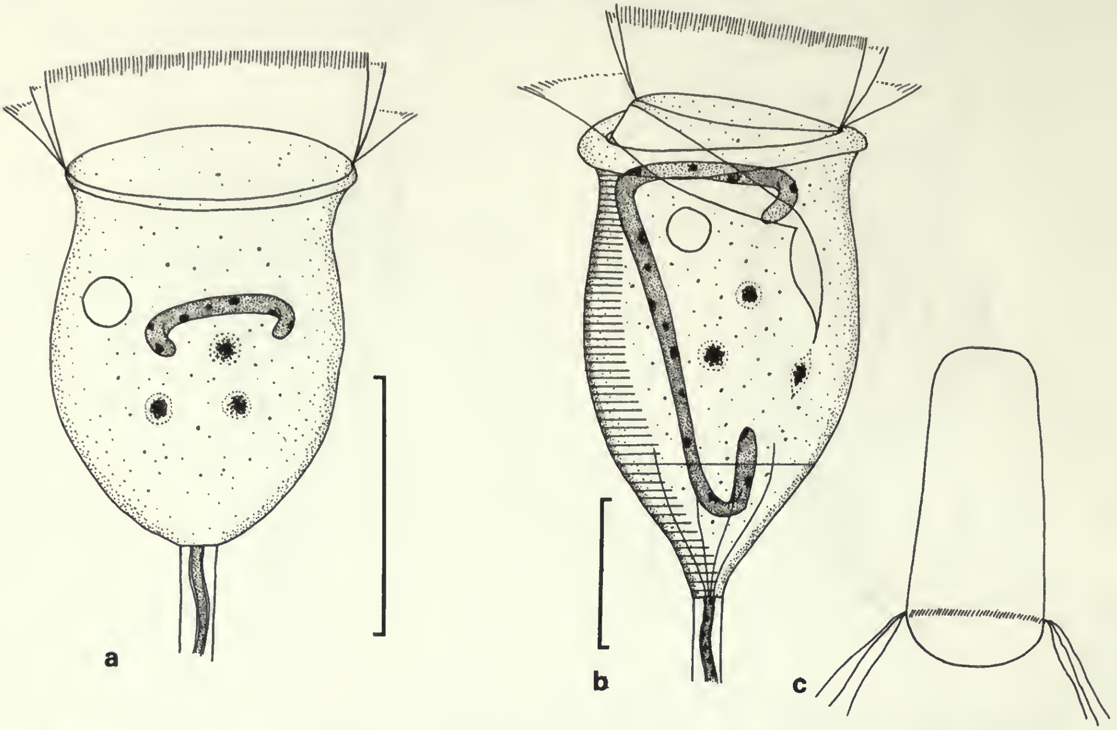

Fig. 13. (a) *V. communis* (after Curds, 1969), bar = 25 µm; (b) *V. convallaria* zooid; (c) telotroch (after Foissner, 1979), bar = 25 µm.

V. chlorostigma Ehrenberg, 1831

V. chlorellata Stiller, 1940

Diagnosis (Fig. 12b). Zooid 55–60 µm long × 25–30 µm wide, almost conical in shape, sometimes with a distinct ridge near the telotroch band and sharply constricted below peristomial lip which measures 30–35 µm across; disc flat and slightly elevated above peristome; infundibulum reaches $\frac{1}{4}$ body length; C.V. situated in upper one-third of body and empties into left hand wall of infundibulum; macronucleus C-shaped and situated longitudinally in zooid; cytoplasm contains numerous endosymbiotic zoochlorellae; pellicle finely striated; stalk up to 600 µm long.

Habitat. Freshwater lakes.

Remarks. An ultrastructural study of the association between *Vorticella* and its endosymbiotic zoochlorellae was made by Graham & Graham (1980).

V. communis Fromentel, 1874

V. subsphaerica Dons 1915

Diagnosis (Fig. 13a). Zooid 30 µm long × 25 µm wide, somewhat rotund and slightly constricted beneath peristomial lip which measures 25 µm in diameter; disc flat; c.v. situated in upper one-third of body; macronucleus C-shaped and lies transversely across centre of zooid; pellicular striations not visible.

Habitat. Freshwater or marine; solitary.

V. convallaria Linnaeus, 1758

V. chinensis Tai, 1931
V. citrina (Müller, 1773) Fauré-Fremiet, 1904

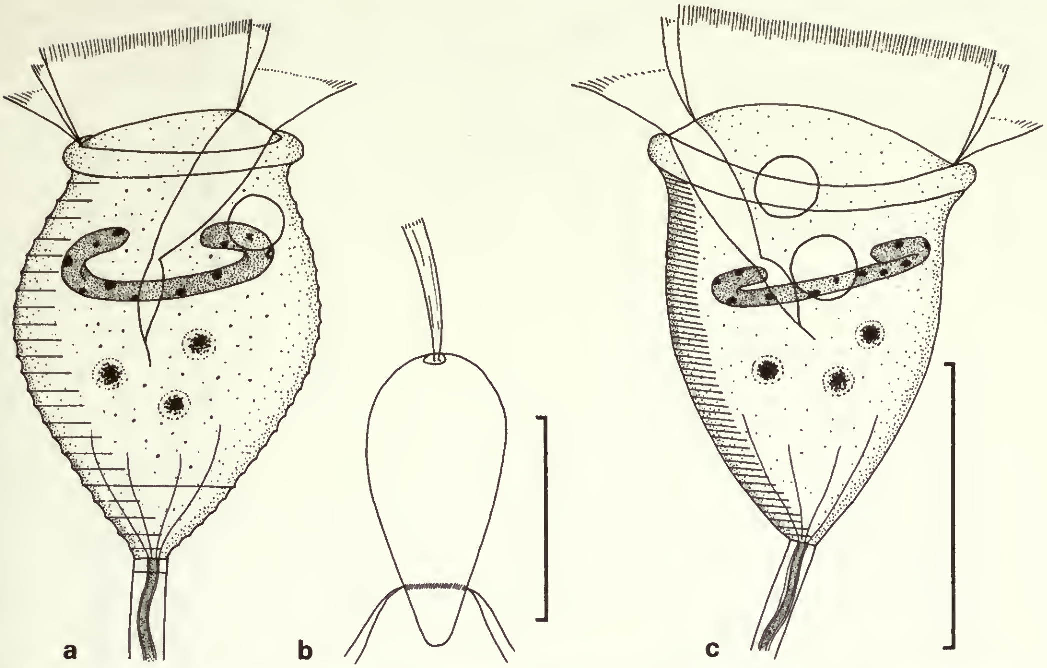

Fig. 14. (a) *V. costata* zooid; (b) telotroch (after Foissner, 1979), bar = 10 µm; (c) *V. dimorpha* (after Stiller, 1940), bar = 25 µm.

V. citrina var. *turgescens* Stiller, 1931
V. convallaria var. *compacta* Nenninger, 1948
V. cothurnata (Hemprich & Ehrenberg, 1828) Ehrenberg, 1838
V. cyathina (Müller) Ehrenberg, 1838
V. cyclopis Kahl, 1933
V. hyalina Stiller, 1940
V. nebulifera var. *similis* (Noland & Finley, 1931) Reid, 1967
V. similis (Stokes, 1887), Reid, 1967

DIAGNOSIS (Figs 13b & c). Zooid 50–95 µm long (mean 77 µm) × 35–55 µm wide (mean 44 µm), inverted bell-shaped and constricted beneath peristomial lip which measures 55–75 µm across (mean 65 µm); disc flat or slightly convex and obliquely elevated; infundibulum reaches one-third body length; C.V. situated in upper one-third of zooid; macronucleus long and J-shaped with upper arm lying horizontally across peristome: pellicle distinctly striated; stalk up to 460 µm long and spasmoneme has numerous thecoplasmic granules.

HABITAT. Freshwater or marine; often forms pseudocolonies; occasionally epibiotic.

REMARKS. For biometric analyses see Reid (1967) and Foissner (1979).

V. costata (Sommer, 1951) Foissner, 1979

V. octava f. *costata* Sommer, 1951

DIAGNOSIS (Figs 14a & b). Zooid 20–28 µm long × 15–20 µm wide and constricted below peristomial lip which measures 15 µm across; disc convex; infundibulum extends to one-third body length; C.V. situated just below peristome and empties into ventral wall of infundibulum; macronucleus C-shaped and lies transversely across centre of zooid; pellicle has concave ribbing between distinct, widely spaced striations; stalk up to 150 µm long; telotroch pyriform with prominent epistomial membrane.

HABITAT. Freshwater.

REMARKS. For biometric analysis see Foissner (1979).

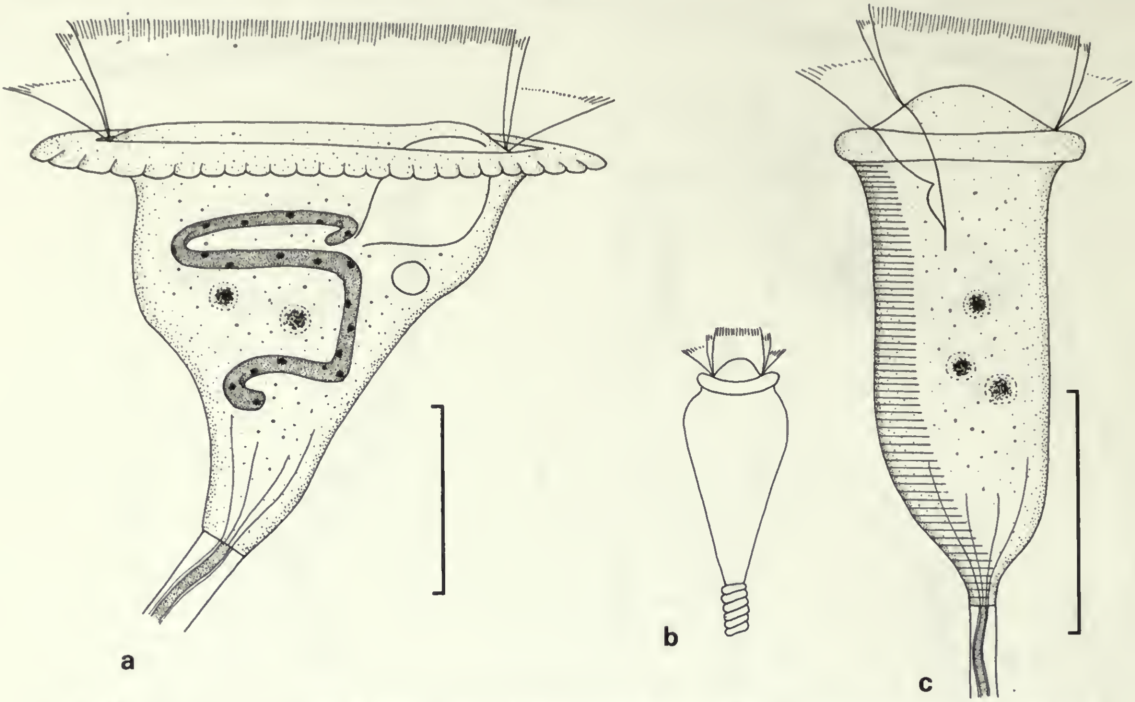

Fig. 15. (a) *V. cratera* (after Küsters, 1974), bar = 25 µm; (b) *V. elongata*, contracted zooid; (c) relaxed zooid (after Fromentel, 1874), bar = 25 µm.

V. cratera Kent, 1881

V. dudekemi Kahl, 1933

Diagnosis (Fig. 15a). Zooid 120 µm long × 100 µm wide, inverted bell-shaped with a broad, flat peristomial lip measuring 150 µm across which has an undulating, frill-like border; infundibulum short; C.V. situated in upper one-third of zooid close to infundibulum; macronucleus long and J-shaped with upper arm lying across peristome; pellicle finely striated; stalk up to 800 µm long.

Habitat. Freshwater or marine; often form pseudocolonies.

V. dimorpha Stiller, 1940

Diagnosis (Fig. 14c). Zooid 32–35 µm long × 15–20 µm wide, variable in shape but usually not constricted below peristomial lip which measures 25 µm across; disc prominently arched above peristome; infundibulum narrow, extending to one-third body length; two C.V.'s situated on either side of infundibulum, the right hand one lying deeper in the cytoplasm, pulses more slowly and is formed by the fusion of two or three smaller vacuoles; macronucleus long, thin, C-shaped and lies diagonally across centre of zooid; pellicle finely striated; stalk slender and up to 70 µm long.

Habitat. Freshwater, originally isolated as an epibiont on *Conchilus unicornis* from Lake Holstein.

V. elongata Fromentel, 1874

V. conica (Stokes, 1887) Noland & Finley, 1931
V. multangula (Fromentel, 1874) Noland & Finley, 1931
V. plicata (Gourret & Roeser, 1886) Noland & Finley, 1931
V. sybcylindrica Ghosh, 1922

Diagnosis (Figs 15b & c). Zooid 60 µm long × 30 µm wide, cylindrical in shape and not constricted beneath peristomial lip which measures 40–45 µm across; disc convex; infundibulum short and broad; pellicle finely striated; upon contraction, peristome only partially closes and cilia are not withdrawn (see Fig. 14c).

Habitat. Freshwater or marine.

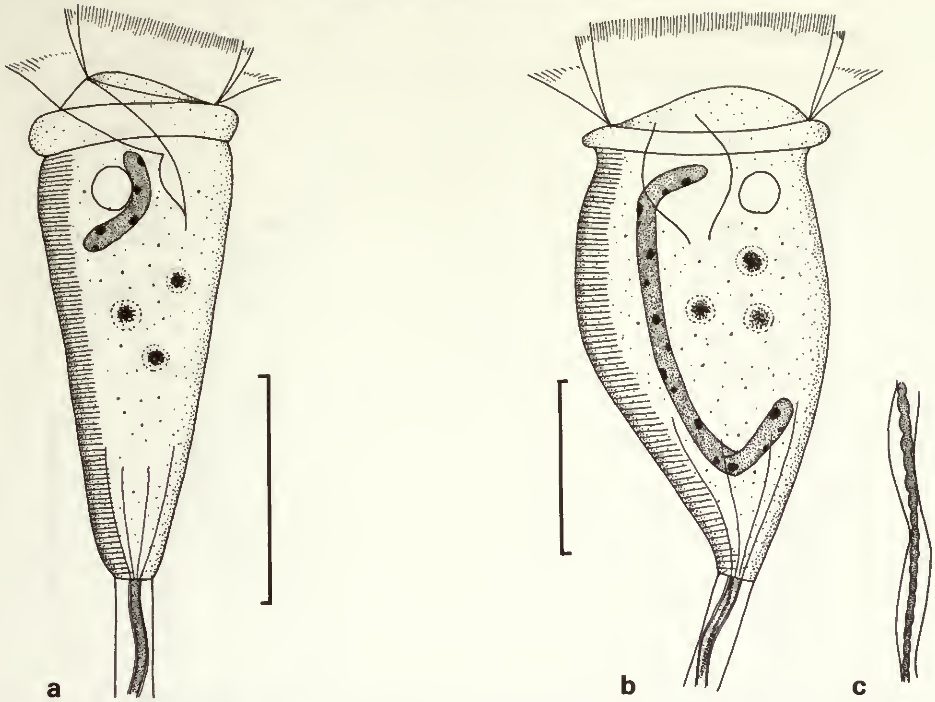

Fig. 16. (a) *V. exilis* (after Nenninger, 1948), bar = 25 µm; (b) *V. flexuosa* zooid, bar = 50 µm; (c) stalk (after Nenninger, 1948).

V. exilis Nenninger, 1948

Diagnosis (Fig. 16a). Zooid 48–60 µm long × 15–20 µm wide, elongate and almost cylindrical in shape but slightly constricted beneath well developed peristomial lip which measures 20 µm across; disc flat and obliquely elevated above peristome; infundibulum short; C.V. lies in niche of macronucleus which is short, thick, slightly curved and situated in upper one-third of body; pellicle distinctly striated; stalk up to 350 µm long.

Habitat. Freshwater, originally isolated as an epibiont on the crustacean *Lestes virus* and the mollusc *Lymnaea stagnalis.*

V. flexuosa Nenninger, 1948

Diagnosis (Figs 16b & c). Zooid 126–144 µm long × 70 µm wide, inverted bell-shaped with slight constriction below peristomial lip which measures 75 µm across; disc prominently arched above peristome; infundibulum short and broad; macronucleus long, C-shaped and lies longitudinally with respect to major axis of body; pellicle finely striated; stalk up to 450 µm long and has a twisted sheath; spasmoneme has single row of thecoplasmic granules.

Habitat. Freshwater, originally isolated as an epibiont on the crustacean *Asellus aquaticus* and *Ricciocarpus natans.*

V. fromenteli (Fromentel, 1874) Kahl, 1935

V. cucullus Fromentel, 1874

Diagnosis (Fig. 17a). Zooid 90 µm long × 30 µm wide, elongated trumpet-shaped and not constricted below peristomial lip which measures 40 µm across; disc prominently arched; infundibulum narrow and reaches one-third of body length; C.V. situated just below peristome; macronucleus C-shaped and lies transversely

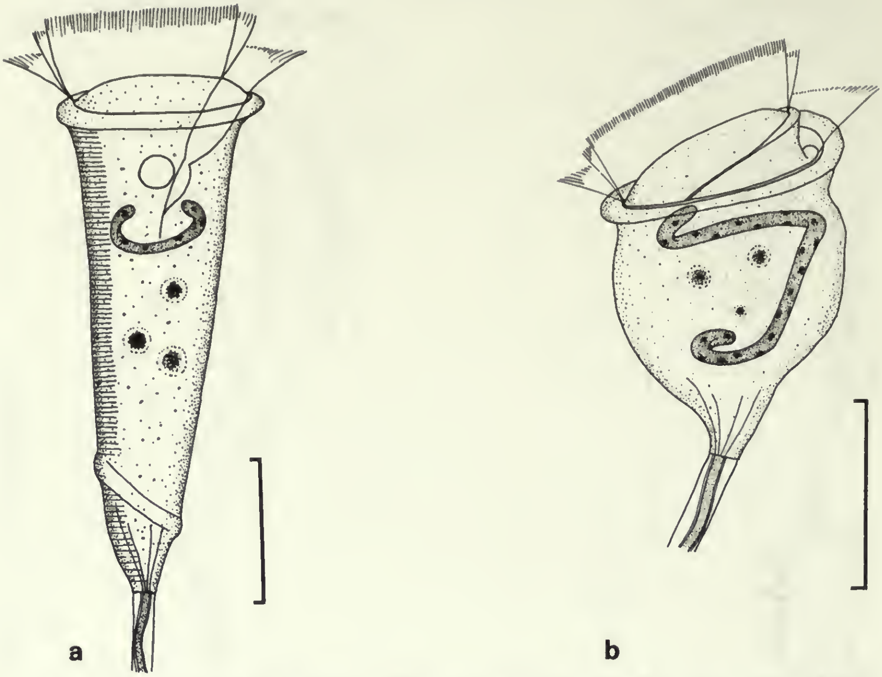

Fig. 17. (a) *V. fromenteli* (after Kahl, 1935), bar = 25 µm; (b) *V. fusca* (after Precht, 1935), bar = 25 µm.

in upper one-third of zoid; pellicle distinctly striated; a single obliquely orientated ridge is present in lower ¼ of zooid.

HABITAT. Freshwater.

V. fusca Precht, 1935

DIAGNOSIS (Fig. 17b). Zooid 88–110 µm long × 65–75 µm wide, inverted bell-shaped with constriction beneath peristome; peristomial lip measures 75 µm across; disc convex and prominently arched above peristome; macronucleus J-shaped; pellicular striations not observed; stalk up to 200 µm long and has numerous thecoplasmic granules.

HABITAT. Marine, originally isolated from the Baltic Sea attached to *Enteromorpha*; typically forms pseudocolonies.

V. globosa Ghosh, 1922

V. urnula Nenninger, 1948

DIAGNOSIS (Fig. 18a). Zooid 25–65 µm long × 20–45 µm wide, somewhat rotund and with a narrow peristomial lip which measures 10 µm across; disc narrow and convex; infundibulum broad and extends to centre of body; c.v. situated in upper part of zooid close to infundibulum; macronucleus C-shaped and lies transversely across centre of zooid; pellicular striations not visible; stalk up to 125 µm long.

HABITAT. Freshwater, originally isolated from pond water near Bengal; occasionally epibiotic.

V. globularia Müller, 1773

V. salina Schmarda, 1854
V. sphaerica d'Udekem, 1864

DIAGNOSIS (Fig. 18b). Zooid 160 µm long × 150 µm wide, spherical in shape with narrow peristomial lip; pellicular striations not visible; stalk up to 1000 µm long.

HABITAT. Freshwater, forms pseudocolonies; occasionally epibiotic.

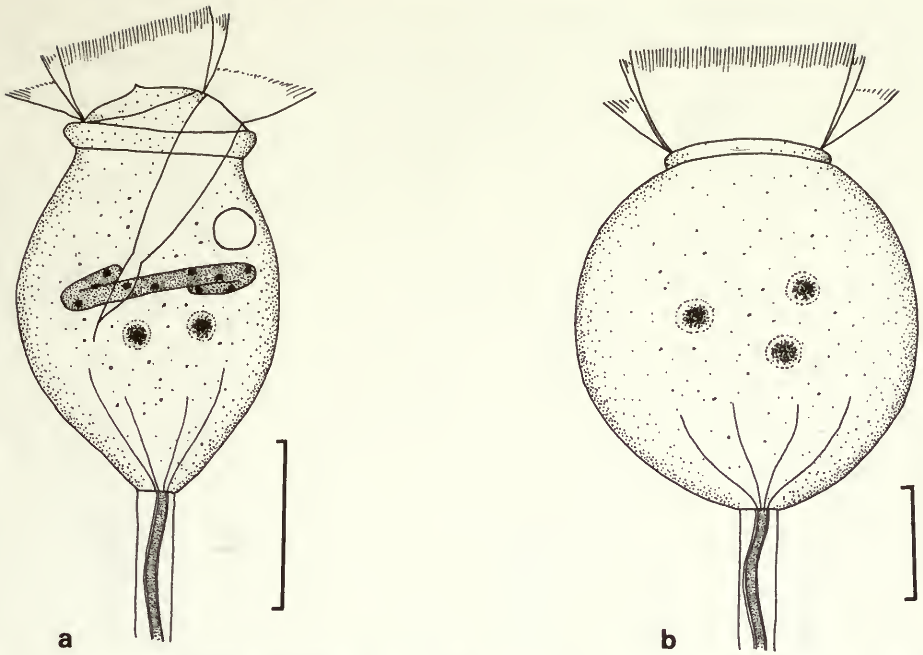

Fig. 18. (a) *V. globosa* (after Nenninger, 1948), bar = 25 μm; (b) *V. globularia* (after Kent, 1880–82), bar = 50 μm.

V. gracilis Dujardin, 1841

DIAGNOSIS (Figs 19a & b). Zooid 50–70 μm long × 25–35 μm wide, elongated trumpet-shaped and not constricted below peristomial lip which measures 35–40 μm across; disc convex and obliquely raised above peristome; infundibulum broad and reaches centre of zooid; C.V. situated just beneath peristome and empties into ventral wall of infundibulum; macronucleus J-shaped and situated longitudinally in body with upper arm lying across peristome; pellicle finely striated and with concave ribbing between striations; stalk up to 350 μm long and has a twisted sheath; thecoplasmic granules are present on spasmoneme; telotroch slender with prominent epistomial membrane.

HABITAT. Freshwater; recently redescribed by Foissner (1979).

V. granulata Kahl, 1933

DIAGNOSIS (Fig. 19c). Zooid 50–60 μm long × 30–35 μm wide, constricted below peristomial lip which measures 20 μm across; disc slightly convex; infundibulum short; C.V. situated in upper one-third of body; macronucleus long, C-shaped and lies longitudinally with respect to major axis of zooid; pellicle finely striated with irregular granules on surface; stalk up to 250 μm long.

HABITAT. Marine.

V. halophila Stiller, 1941

DIAGNOSIS (Fig. 20a). Zooid 40–50 μm long × 30–35 μm wide, inverted bell-shaped and constricted below wide peristomial lip which measures 38–40 μm across; two C.V.'s situated in peristomial region, both emptying into left hand wall of infundibulum; macronucleus long and slender and lies longitudinally with respect to major axis of zooid; pellicle distinctly striated and has convex ribbing between striations; stalk up to 250 μm long.

HABITAT. Freshwater, often attached to detritus where it may form large pseudocolonies.

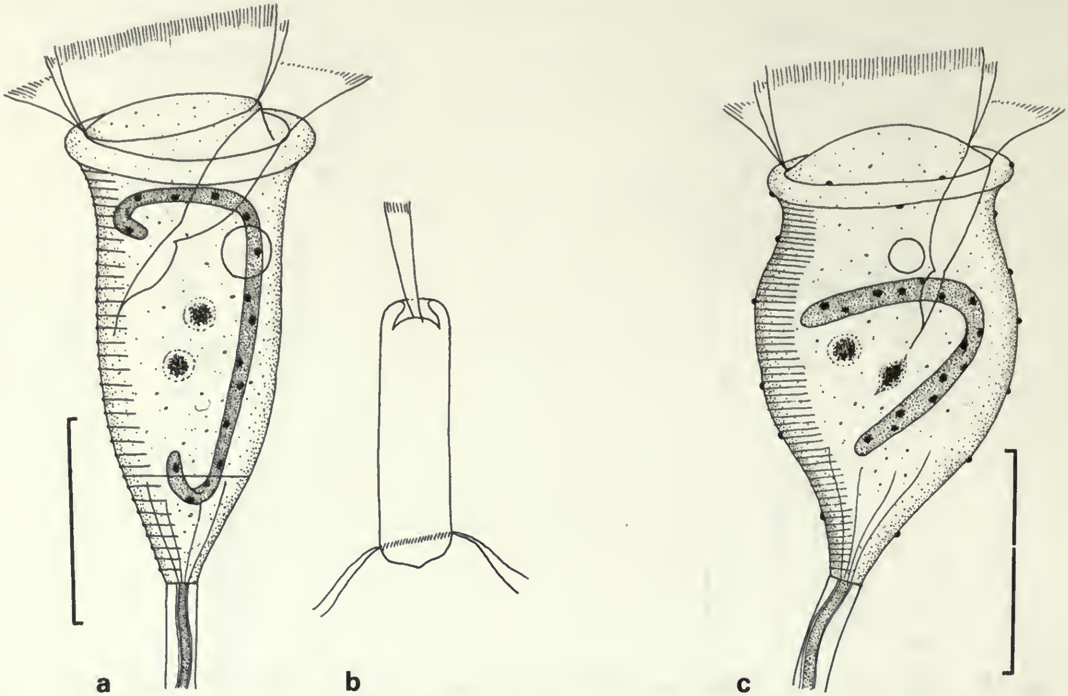

Fig. 19. (a) *V. gracilis* zooid; (b) telotroch (after Foissner, 1979), bar = 25 μm; (c) *V. granulata* (after Stiller, 1935), bar = 25 μm.

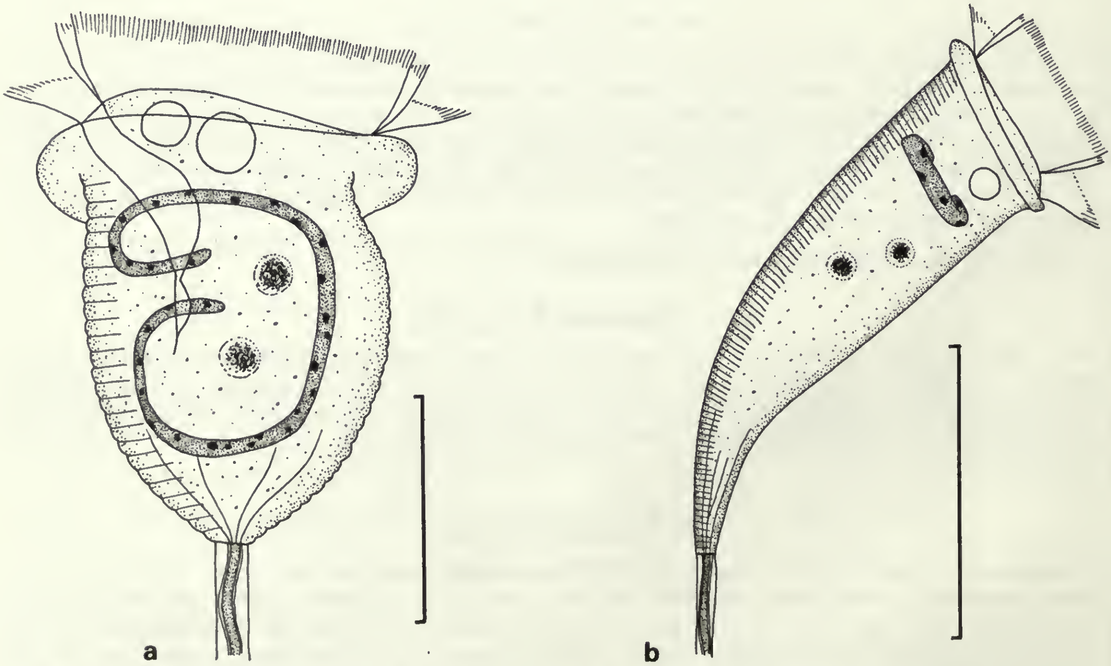

Fig. 20. (a) *V. halophila* (after Stiller, 1941), bar = 25 μm; (b) *V. hamata* (after Kahl, 1935), bar = 25 μm.

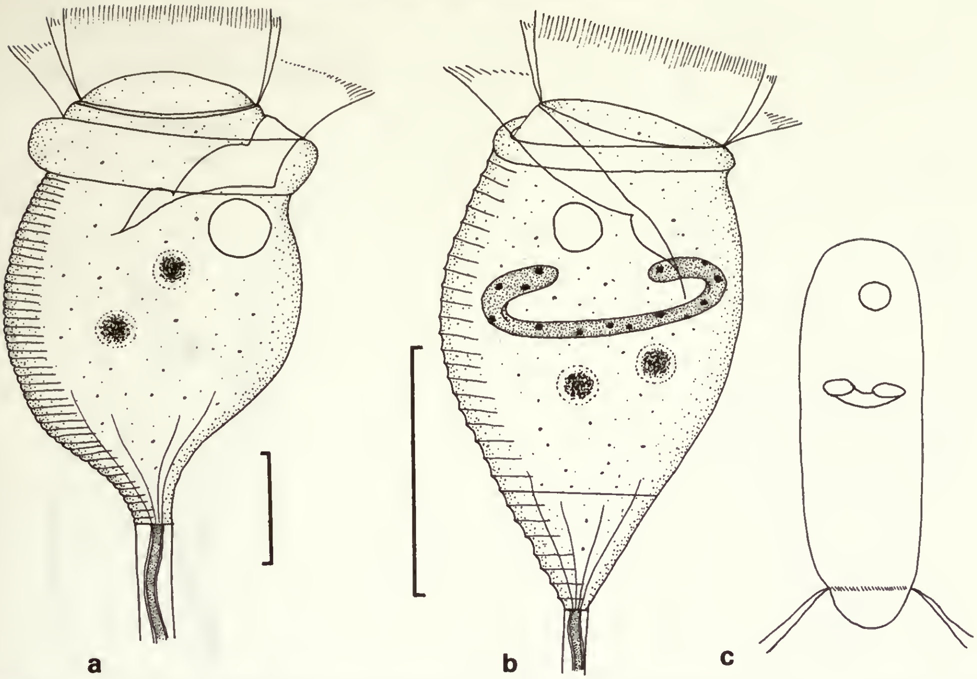

Fig. 21. (a) *V. incisa* (after Stiller, 1938), bar = 25 µm; (b) *V. infusionum* zooid; (c) telotroch (after Küsters, 1974), bar = 25 µm.

V. hamata Ehrenberg, 1831

V. delicatulata Biernacka, 1963

Diagnosis (Fig. 20b). Zooid 40 µm long × 15 µm wide, elongate and typically curved though not constricted below peristomial lip which measures 18 µm across; disc flat and obliquely elevated above peristome; C.V. situated just beneath peristome; macronucleus C-shaped and lies transversely across upper one-third of body; pellicle faintly striated.

Habitat. Marine or freshwater; solitary.

V. incisa Stiller, 1938

Diagnosis (Fig. 21a). Zooid 65–80 µm long × 50–55 µm wide and sharply constricted below peristomial lip which measures 50–60 µm across; disc prominently arched above peristome; infundibulum short and broad; C.V. situated just below peristome and empties into ventral wall of infundibulum via a short channel; macronucleus C-shaped and lies transversely across upper part of body; pellicle finely striated and has convex ribbing between the striations; stalk up to 150 µm long; thecoplasmic granules are present on spasmoneme.

Habitat. Freshwater, forming large pseudocolonies.

V. infusionum Dujardin, 1841

V. abbreviata (Keiser, 1921) Kahl, 1935
V. striata var. *octava* f. *utriculus* (Stokes 1885) Noland & Finley, 1931
V. utriculus (Stokes, 1885) Noland & Finley, 1931

Diagnosis (Figs 21b & c). Zooid 35–60 µm long × 18–30 µm wide, constricted beneath peristomial lip which measures 15–20 µm across; infundibulum short; C.V. situated just below peristome; macronucleus C-shaped and lies transversely across centre of body; pellicle distinctly striated and has concave ribbing.

Habitat. Freshwater or marine.

Remarks. Redescribed with biometric analysis by Foissner (1979).

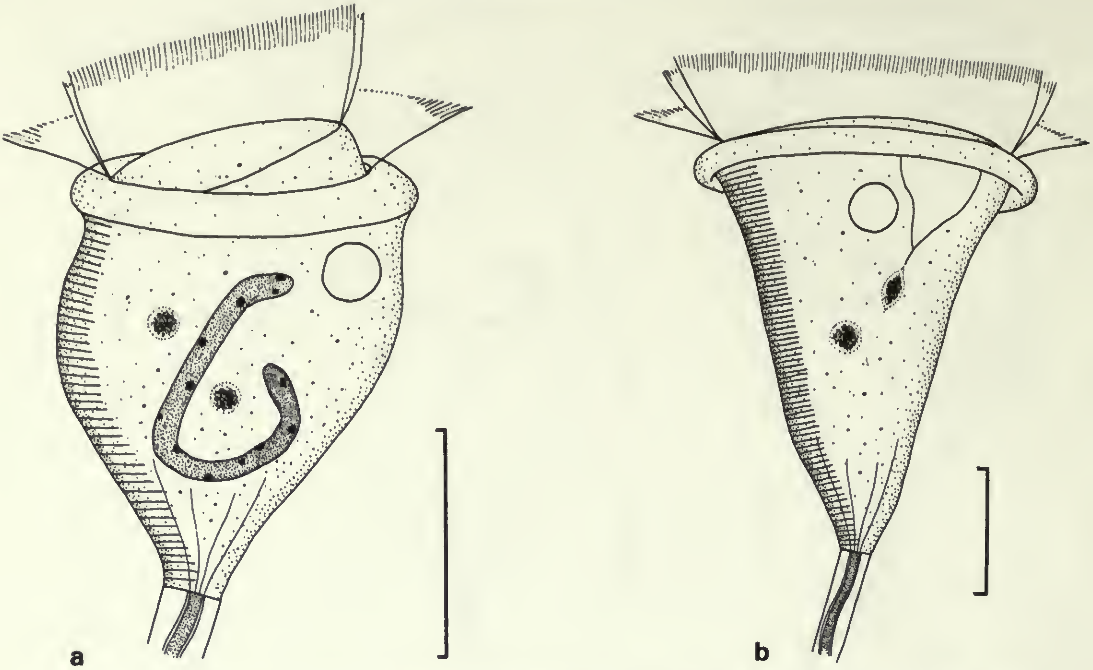

Fig. 22. (a) *V. jaerae* (after Precht, 1935), bar = 25 μm; (b) *V. kenti* (after Stiller, 1938), bar = 50 μm.

V. jaerae Precht, 1935

Diagnosis (Fig. 22a). Zooid 40–53 μm long × 30–40 μm wide, inverted bell-shaped and constricted below peristomial lip which measures 35–40 μm across; disc flat and obliquely elevated above peristome; C.V. situated in upper one-third of body; macronucleus long, irregularly shaped and twisted; pellicle distinctly striated; stalk up to 120 μm long.

Habitat. Marine, forming pseudocolonies attached to the crustacean *Jaera marina*.

V. kenti (Kent, 1881) Kahl, 1935

V. floridensis Stokes, 1886
V. spectrabilis Kent, 1881

Diagnosis (Fig. 22b). Zooid 170 μm long × 60 μm wide, elongated trumpet-shaped and not constricted below peristomial lip which measures 100–120 μm across; disc flat; infundibulum short; C.V. situated just beneath peristome; pellicle finely striated; stalk up to 500 μm long.

Habitat. Freshwater ponds, often forming large pseudocolonies.

V. latifunda Nenninger, 1948

Diagnosis (Fig. 23a). Zooid 60 μm long × 30 μm wide, barrel-shaped and constricted below thick peristomial lip which measures 30 μm across; disc flat and slightly elevated; infundibulum reaches $\frac{1}{4}$ body length; C.V. situated in upper one-third of zooid; macronucleus thick, C-shaped and lies transversely across centre of zooid; pellicle finely striated; stalk up to 420 μm long.

Habitat. Freshwater, originally found as an epibiont attached to the crustaceans *Lestes sponsa* and *L. virens*.

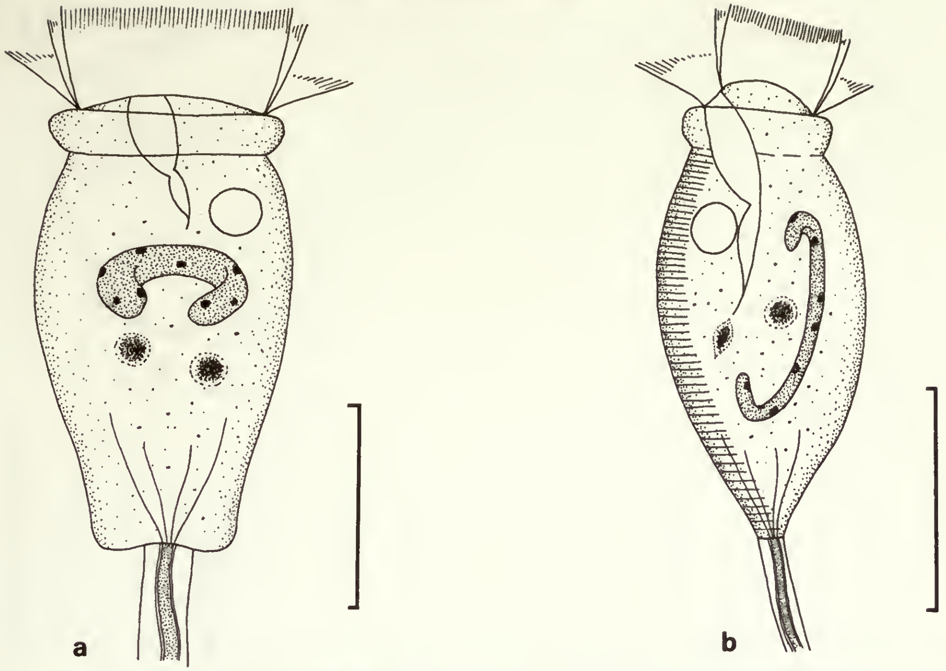

Fig. 23. (a) *V. latifunda* (after Nenninger, 1948), bar = 25 µm; (b) *V. lichenicola* (after Penard, 1922), bar = 25 µm.

V. lichenicola Greeff, 1888

V. inconstantans Green, 1974.

Diagnosis (Fig. 23b). Zooid 50–65 µm long × 25–30 µm wide, somewhat elongate and constricted beneath peristomial lip which measures 20 µm across; infundibulum reaches centre of body; C.V. situated in upper one-third of zooid, close to infundibulum; macronucleus irregular or C-shaped and usually lies longitudinally in lower $\frac{1}{2}$ of body; pellicle finely striated; stalk up to 65 µm long.

Habitat. Freshwater, attached to lichen, mosses or sand particles and occasionally epibiotic attached to the crustacean *Macrothrix hirsuticornis.*

V. lima Kahl, 1933

Pseudovorticella lima (Kahl, 1933) Jankowski, 1976.

Diagnosis (Fig. 24a). Zooid 60–70 µm long × 30 µm wide, usually curved and constricted beneath well developed peristomial lip which measures 25 µm across; disc convex and slightly elevated above peristome; infundibulum short; C.V. lies in upper one-third of body close to ventral wall of infundibulum; macronucleus long, C-shaped and situated longitudinally with respect to major axis of body; pellicle distinctly striated with concave ribbing between the striations, and furnished with small refractile granules.

Habitat. Marine.

V. limnetis Stokes, 1885

Diagnosis (Fig. 24b). Zooid 50 µm long × 35 µm wide, inverted bell-shaped and constricted below peristomial lip which measures 35 µm across; disc convex and obliquely elevated above peristome; infundibulum broad and reaches one-third body length; C.V. lies beneath peristome and empties into ventral wall of infundibulum; macronucleus C-shaped and lies transversely across centre of body; pellicle distinctly striated with concave ribbing between striations; stalk sheath twisted.

Habitat. Freshwater.

Remarks. Redescribed with biometric analysis by Foissner (1979).

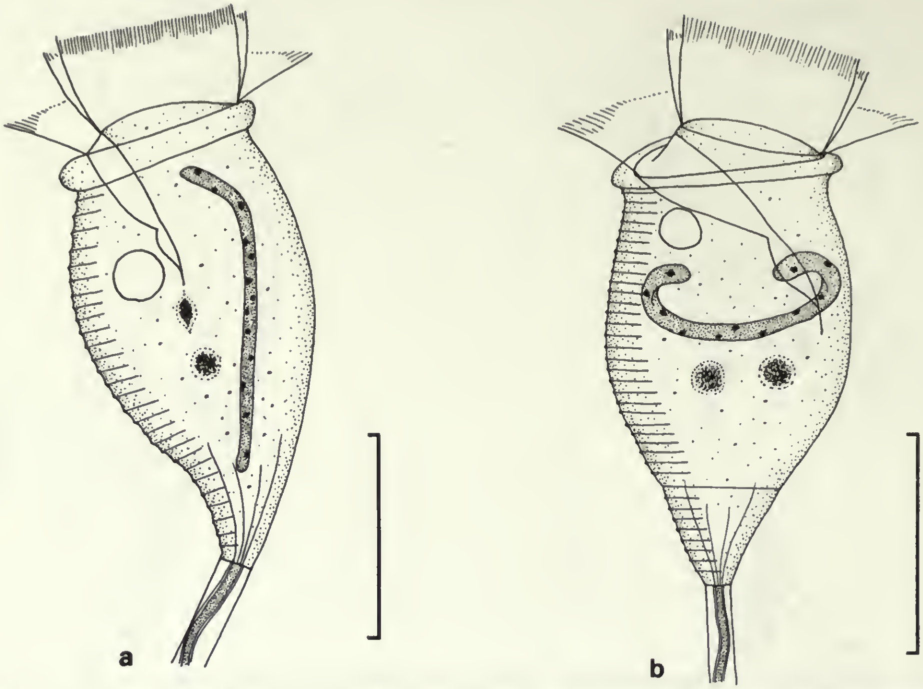

Fig. 24. (a) *V. lima* (after Kahl, 1935), bar = 25 µm; (b) *V. limnetis* (after Foissner, 1979), bar = 25 µm.

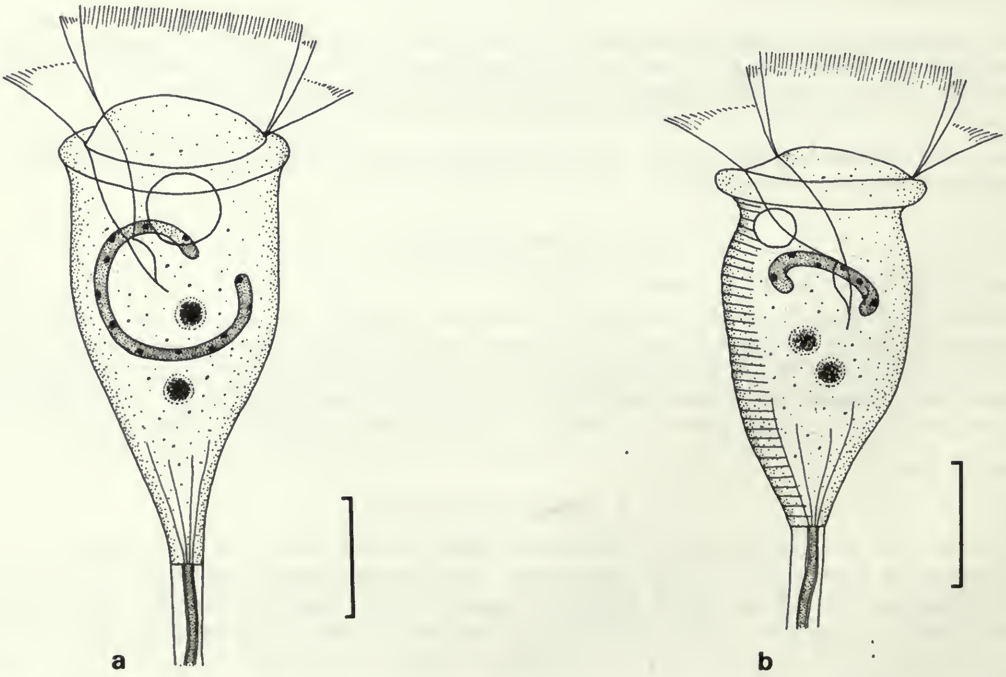

Fig. 25. (a) *V. longifilum* (after Stiller, 1971), bar = 25 µm; (b) *V. longiseta* (after Dietz, 1964), bar = 25 µm.

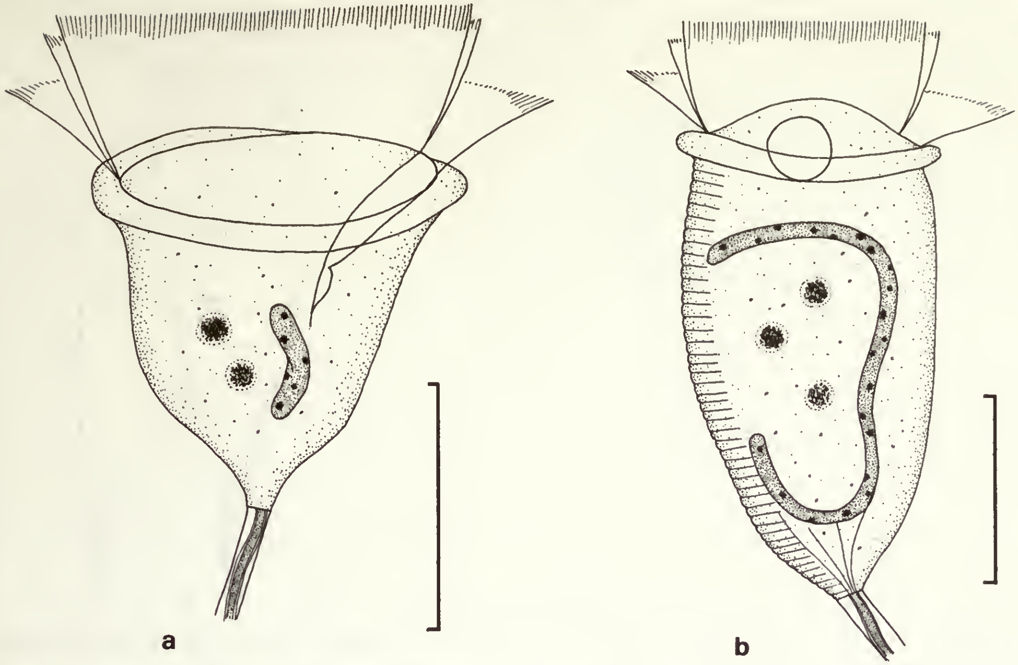

Fig. 26. (a) *V. longitricha* (after Gajewskaja, 1933), bar = 25 µm; (b) *V. lutea* (after Stiller, 1938), bar = 50 µm.

V. longifilum Kent, 1881

V. crassicaulis Nenninger, 1948
V. longifilum f. *epizooicum* Szczepanowski, 1978
V. macrocaulis (Stokes, 1885) Noland & Finley, 1931
V. simplex Nenninger, 1948

Diagnosis (Fig. 25a). Zooid 80–90 µm long × 30–35 µm wide, inverted bell-shaped with constriction below peristomial lip which measures 45 µm across; disc prominently arched above peristome; infundibulum short; C.V. lies beneath peristomial lip; macronucleus C-shaped and situated longitudinally in upper two-thirds of body; pellicular striations not visible; stalk slender and up to 1000 µm long.

Habitat. Freshwater, solitary; occasionally epibiotic.

V. longiseta Dietz, 1964

Diagnosis (Fig. 25b). Zooid 82 µm long × 50 µm wide, elongate and constricted below peristomial lip which measures 65 µm across; disc flat and obliquely elevated; infundibulum broad and reaches one-third body length; C.V. lies beneath peristome and empties into infundibulum via short channel; macronucleus C-shaped and situated transversely across centre of zooid; pellicle finely striated with convex ribbing between striations.

Habitat. Marine.

V. longitricha Gajewskaja, 1933

Diagnosis (Fig. 26a). Zooid 30 µm long × 25 µm wide, inverted bell-shaped with no constriction below peristomial lip which measures 30–35 µm across; disc prominently arched above peristome; infundibulum reaches one-third body length; C.V. situated just below peristome and empties into infundibulum; macronucleus short, C-shaped and lies longitudinally in centre of zooid; pellicle finely striated; stalk up to 90 µm long.

Habitat. Marine, originally found as an epibiont attached to gammarids.

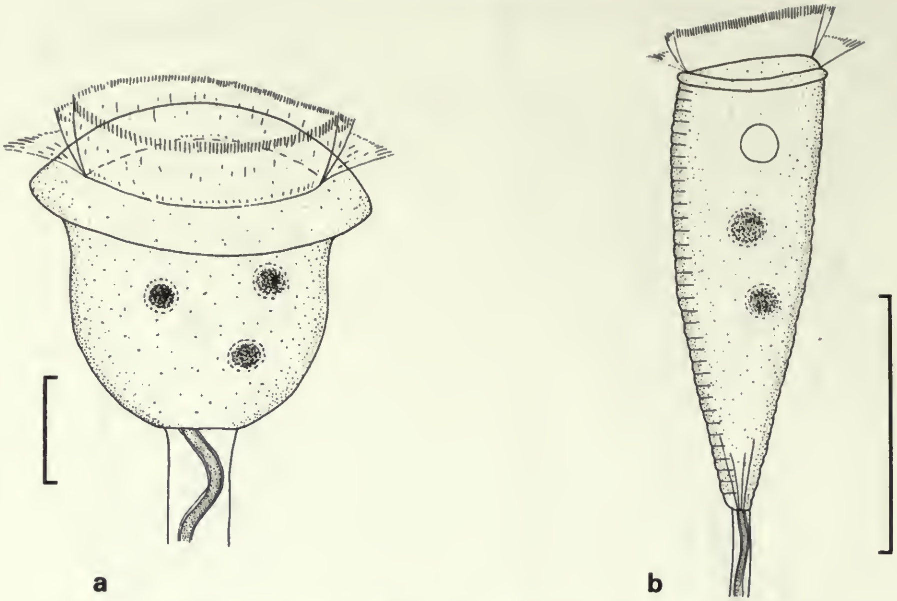

Fig. 27. (a) *V. lymnaearum* (after Viljoen & As, 1983), bar = 10 µm; (b) *V. macrophya* (after Stokes, 1885*b*), bar = 25 µm.

V. lutea Stiller, 1938

Diagnosis (Fig. 26b). Zooid 140 µm long × 75–80 µm wide and almost cylindrical in shape; peristomial lip 80–90 µm across; disc convex; infundibulum reaches one-third body length; C.V. situated just beneath peristome and empties into dorsal wall of infundibulum; macronucleus long, J-shaped and situated longitudinally with respect to major axis of body; pellicle distinctly striated and with convex ribbing between striations; stalk up to 700 µm long.

Habitat. Freshwater, originally found attached to the pond weed *Myriophylum*.

V. lymnaearum Viljoen & As, 1983

Diagnosis (Fig. 27a). Zooid 26–30 µm long (mean 28·3 µm) × 25–35 µm wide (mean 29·0 µm), inverted bell-shaped with a broad peristomial lip (45 µm in diameter); peristomial disc convex; macronucleus C-shaped and lies horizontally with respect to major body axis; pellicle striated.

Habitat. Freshwater, originally isolated from Westdene Dam, Johannesburg, South Africa attached to the shell of the mollusc, *Lymnaea natalensis*.

V. macrophya Stokes, 1885

Diagnosis (Fig. 27b). Zooid 38 µm long × 15–20 µm wide, elongate and almost cylindrical in shape; not constricted beneath peristomial lip which measures 15–20 µm across; disc flat and obliquely elevated; macronucleus short, C-shaped and lies in upper one-third of body; pellicle finely striated with convex ribbing between striations; stalk up to 60 µm long.

Habitat. Freshwater, originally isolated from pond water in North America; solitary.

V. macrostyla Schmarda, 1854

Diagnosis (Fig. 28a). Zooid 50 µm long × 30 µm wide, barrel-shape with a narrow peristomial lip which measures 20–25 µm in diameter; pellicle with up to 100 striations; stalk 750–1000 µm long.

Habitat. Freshwater.

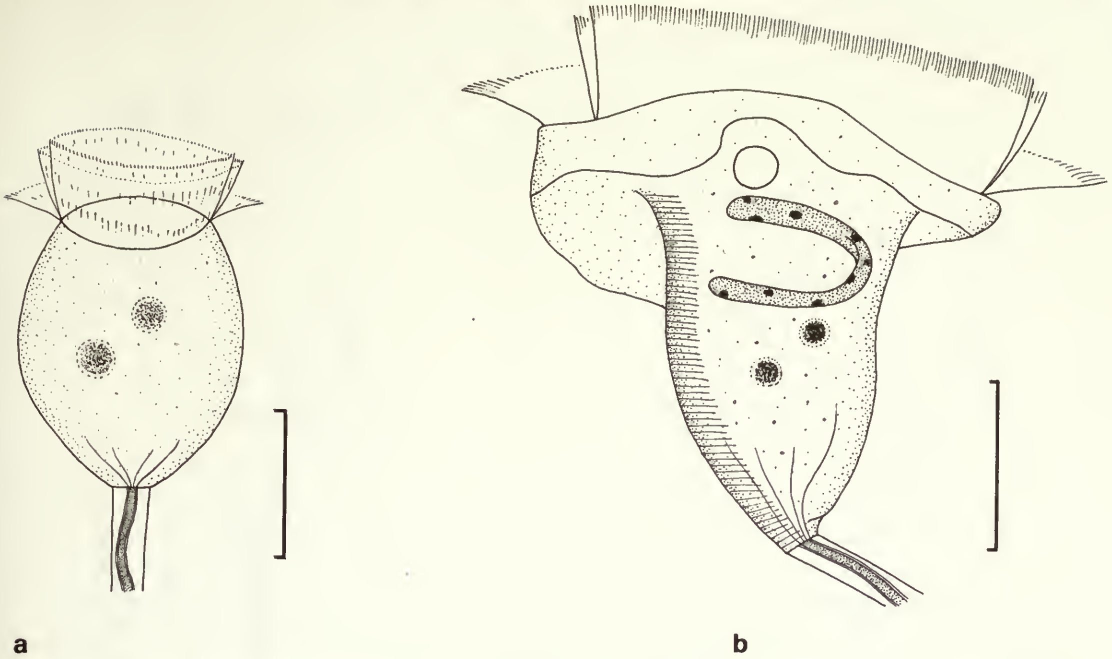

Fig. 28. (a) *V. macrostyla* (after Schmarda, 1854), bar = 25 µm; (b) *V. marginata* (after Stiller, 1931), bar = 25 µm.

V. marginata Stiller, 1931

V. marginata f. *poliensis* (Stiller) Szczepanowski, 1978
V. marginata f. *minor* (Stiller) Szczepanowski, 1978

Diagnosis (Fig. 28b). Zooid 70–90 µm long × 32–45 µm wide, elongate and slightly constricted below peristomial lip which is thin but very wide measuring 100–110 µm across; disc broad, flat and obliquely elevated above peristome; infundibulum short, broad and lies almost horizontally across peristomial region; C.V. empties into right hand wall of infundibulum; macronucleus long, C-shaped and situated transversely in upper $\frac{1}{2}$ of body; pellicle finely striated; stalk up to 270 µm long.

Habitat. Freshwater.

V. marina Greeff, 1870

V. minuta Precht, 1935

Diagnosis (Fig. 29a). Zooid 35–65 µm long × 40–50 µm wide, inverted bell-shaped and sharply constricted below peristomial lip which measures 40–50 µm across; disc flat and obliquely elevated above peristome; infundibulum short; C.V. large and situated just beneath peristome; macronucleus long, C-shaped and lies transversely across centre of zooid; pellicle distinctly striated; stalk up to 300 µm long.

Habitat. Marine; forms pseudocolonies.

Remarks. This species has been redescribed by Stiller (1935) and Küsters (1974).

V. mayeri Fauré-Fremiet, 1920

Pelagovorticella mayeri (Fauré-Fremiet, 1920) Jankowski, 1980.

Diagnosis (Fig. 30). Zooid 35 µm long × 30 µm wide, sharply curved and constricted beneath peristomial lip which measures 25 µm across; disc convex and elevated obliquely above peristome; infundibulum broad and reaches centre of zooid; macronucleus C-shaped and lies transversely across centre of zooid; pellicle

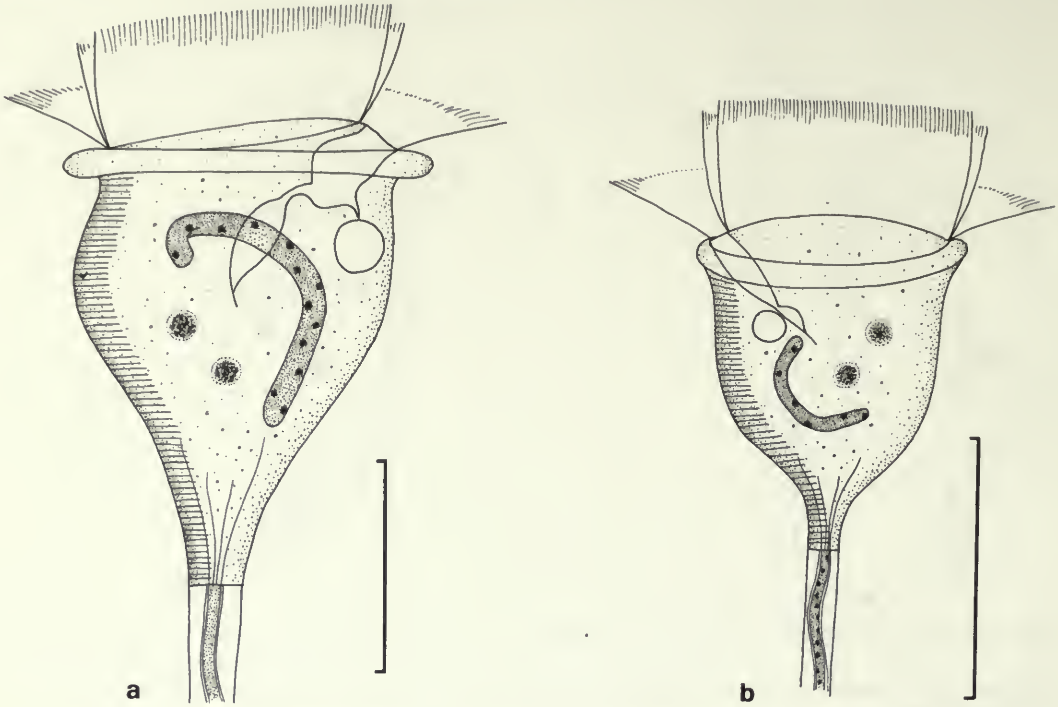

Fig. 29. (a) *V. marina* (after Küsters, 1974), bar = 25 μm; (b) *V. microscopica* (after Stiller, 1971), bar = 10 μm.

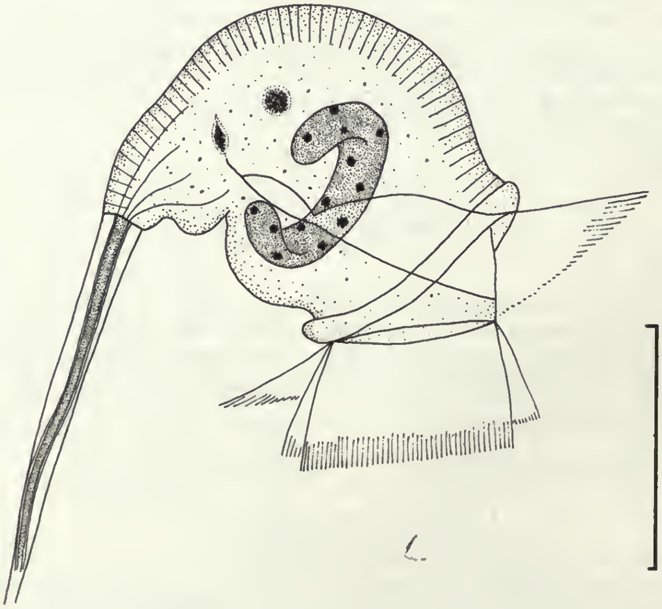

Fig. 30. *V. mayeri* (after Fauré-Fremiet, 1920), bar = 25 μm.

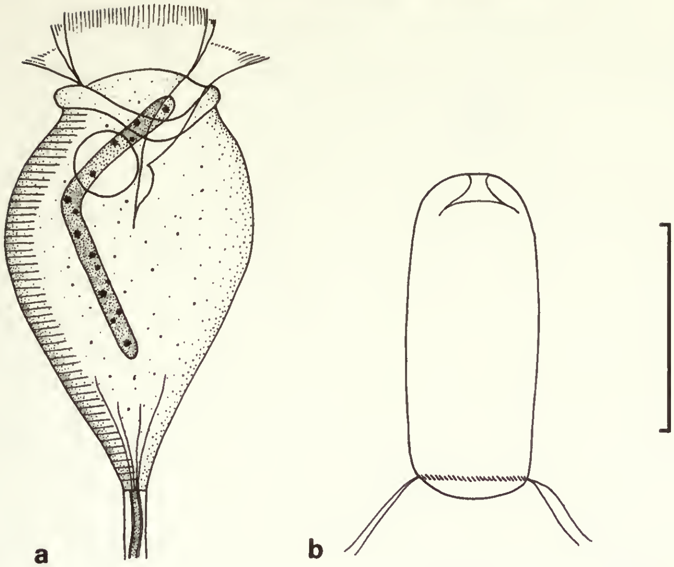

Fig. 31. (a) *V. microstoma* zooid; (b) telotroch (after Noland & Finley, 1931), bar = 25 µm.

distinctly striated; stalk up to 140 µm long and is never attached to a substratum but is used like a giant flagellum to aid swimming.

HABITAT. Marine or freshwater; pelagic.

V. microscopica Fromentel, 1874

DIAGNOSIS (Fig. 29b). Zooid 12 µm long × 8·0 µm wide, inverted bell-shaped but not constricted below peristomial lip which measures 10 µm across; pellicle striated; spasmoneme has red thecoplasmic granules.

HABITAT. Freshwater.

V. microstoma Ehrenberg, 1830

V. chydoricola Šramek-Hušek, 1946
V. constricta (Fromentel, 1874) Noland & Finley, 1931
V. cupifera (Kahl, 1935) Pratt & Rosen, 1983
V. cyclopicola Kahl, 1935
V. fluvialis (Fromentel, 1874) Noland & Finley, 1931
V. longimacronucleata Fukui & Morishita, 1961
V. magna Fukui & Morishita, 1961
V. mammillata (Fromentel, 1874) Noland & Finley, 1931
V. microstoma var. *defluviatilis* Nenninger, 1948
V. microstoma f. *turgescens* Stiller
V. partita Fukui & Morishita, 1961
V. pileolata Lepsi, 1948
V. submicrostoma Ghosh, 1922

DIAGNOSIS (Fig. 31). Zooid 35–96 µm long (mean 55 µm) × 22–50 µm wide (mean 35 µm), constricted beneath peristomial lip which measures 12–25 µm across (mean 23 µm); disc convex; infundibulum reaches one-third body length; C.V. empties into ventral wall of infundibulum; macronucleus long, C-shaped and lies longitudinally with respect to major axis of body; pellicle distinctly striated; stalk up to 380 µm long (mean 90 µm) × 1·5–4·0 µm wide (mean 3·0 µm).

HABITAT. Freshwater, especially stagnant waters, activated sludge and areas of high organic content; occasionally epibiotic.

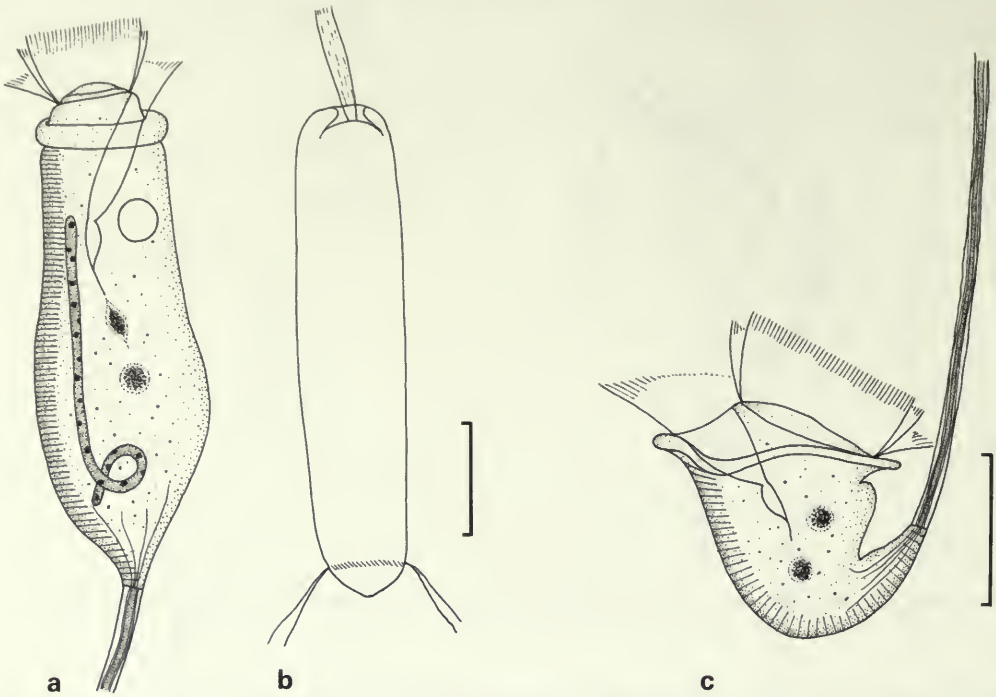

Fig. 32. (a) *V. muralis* zooid; (b) telotroch (after Penard, 1922), bar = 25 µm; (c) *V. natans* (after Fauré-Fremiet, 1924), bar = 50 µm.

V. muralis Penard, 1922

DIAGNOSIS (Figs 32a & b). Zooid 90–125 µm long × 35–45 µm wide, elongate but with distinct bulge in distal part of body and constricted below peristomial lip which measures 25 µm across; disc narrow and prominently arched above peristome; infundibulum reaches one-third body length; C.V. lies just beneath peristome and close to infundibulum; macronucleus long, straight with ends folded back, and situated longitudinally with respect to major axis of body; pellicle finely striated; stalk slender and up to 100 µm long.

HABITAT. Freshwater and *Sphagnum* bogs.

V. natans Fauré-Fremiet, 1924

DIAGNOSIS (Fig. 32c). Zooid 100 µm long × 50 µm wide, inverted bell-shape though curved and slightly constricted below peristomial lip which measures 75 µm across; disc convex and prominently arched above peristome; pellicle distinctly striated; stalk up to 700 µm long and never attached to a substratum; animal swims by means of oral ciliature with stalk held projecting forwards.

HABITAT. Freshwater, pelagic.

V. nutans Müller, 1773

V. gemella (Fromentel, 1874) Noland & Finley, 1931
V. procumbens (Fromentel, 1874) Noland & Finley, 1931

DIAGNOSIS (Fig. 33a). Zooid 60–80 µm long × 25–30 µm wide, elongate and held in characteristic nodding position on stalk; body constricted below peristomial lip which measures 30 µm across; disc prominently arched above peristome; C.V. situated in upper one-third of body; macronucleus long, thin and lies longitudinally with respect to major axis of body; pellicular striations not visible; stalk up to 320 µm long.

HABITAT. Freshwater or marine.

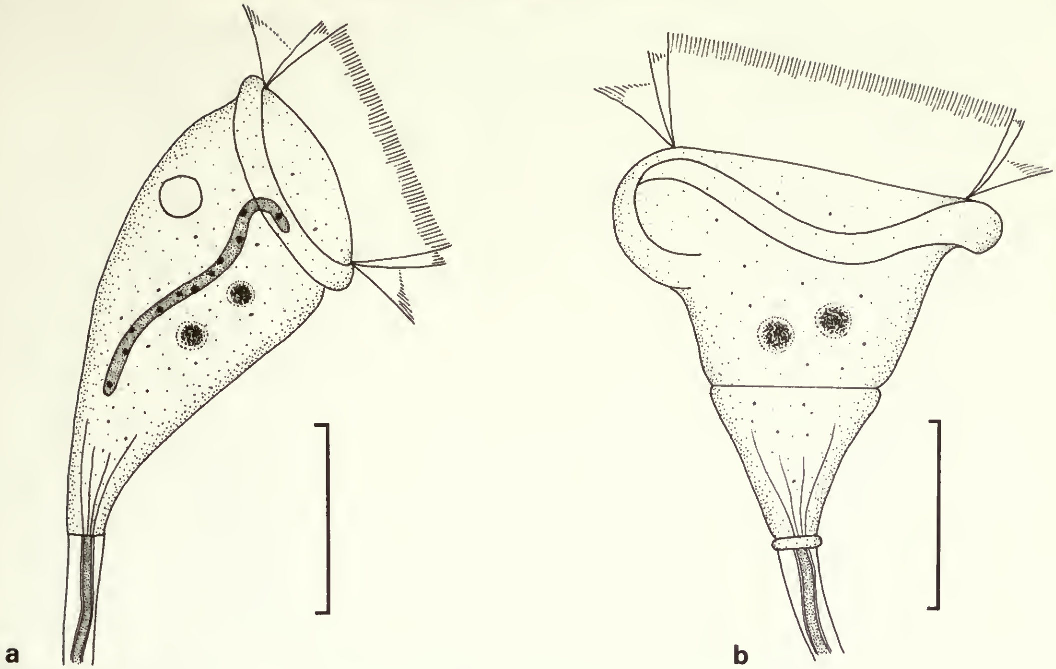

Fig. 33. (a) *V. natans* (after Curds, 1969), bar = 25 µm; (b) *V. obconica* (after Dons, 1915), bar = 25 µm.

V. obconica (Dons, 1915) Kahl, 1935

V. conica Dons, 1915

Diagnosis (Fig. 33b). Zooid 55 µm long × 45 µm wide, inverted bell-shaped but not constricted below peristomial lip which measures 55 µm across; pellicle has distinct ridge in region of telotroch band; stalk up to 90 µm long.

Habitat. Marine.

V. operculariformis Foissner, 1979

Diagnosis (Fig. 34a). Zooid 45–55 µm long × 30–50 µm wide, constricted below peristomial lip which measures 15 µm across; disc convex; infundibulum short; C.V. situated in upper one-third of body and empties into ventral wall of infundibulum; macronucleus C-shaped, curved in ring-like manner and lies transversely across the centre of the zooid; pellicle distinctly striated with concave ribbing between the striations; stalk up to 250 µm long.

Habitat. Freshwater, originally isolated from rainwater pools.

V. ovum Dons, 1918

V. incerta Nenninger, 1948.

Diagnosis (Fig. 34b). Zooid 90 µm long × 50–55 µm wide, somewhat rotund and constricted beneath peristomial lip which measures 35 µm in diameter; disc slightly convex; c.v. lies in upper $\frac{1}{2}$ of body; pellicular striations not visible; stalk up to 7·0 µm wide × 90 µm long (see remarks).

Habitat. Marine or freshwater, occasionally epibiotic.

Remarks. The original description was made from a partially contracted specimen.

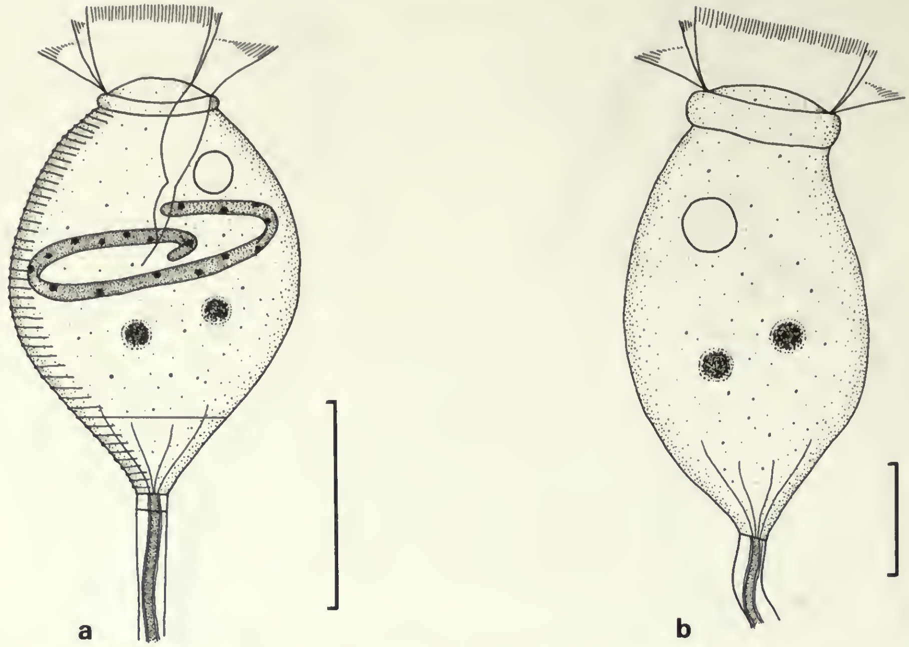

Fig. 34. (a) *V. operculariformis* (after Foissner, 1979), bar = 25 µm; (b) *V. ovum* (after Dons, 1918), bar = 25 µm.

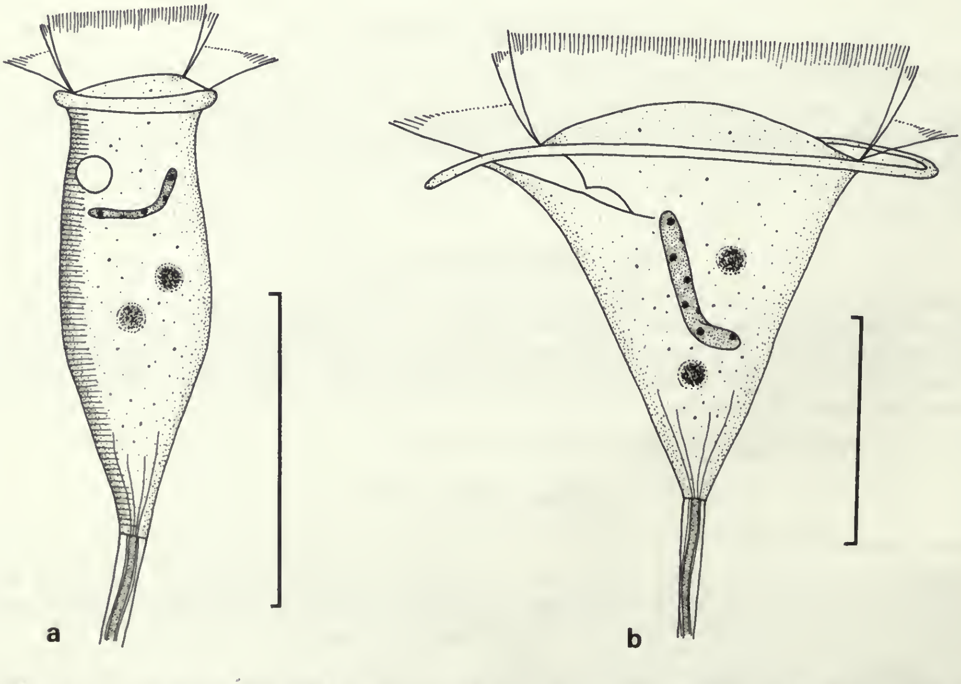

Fig. 35. (a) *V. parasita* (after Stokes, 1887*b*), bar = 25 µm; (b) *V. patellina* (after Kent, 1880–82), bar = 25 µm.

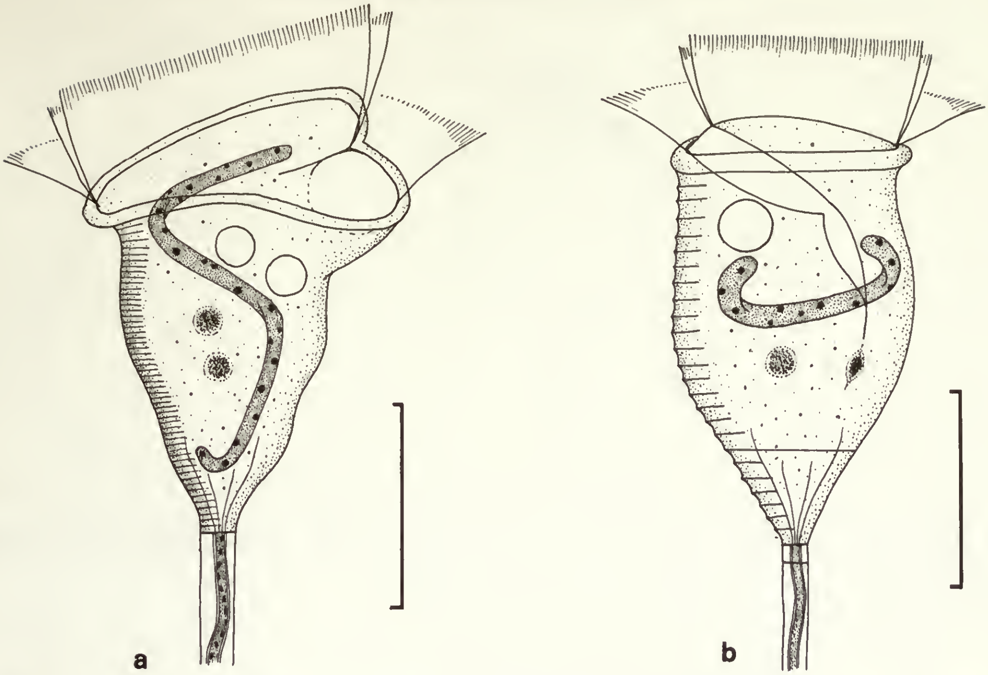

Fig. 36. (a) *V. picta* (after Noland & Finley, 1931), bar = 25 µm; (b) *V. platysoma* (after Foissner, 1979), bar = 10 µm.

V. parasita Stokes, 1887

V. ephemerae Kahl, 1935

Diagnosis (Fig. 35a). Zooid 40 µm long × 10 µm wide, elongate and constricted beneath peristomial lip which measures 15 µm in diameter; disc flat and obliquely elevated above peristome; c.v. situated in upper one-third of body; macronucleus C-shape and lies transversely across upper one-third of body; pellicle finely striated; stalk up to 150 µm long.

Habitat. Freshwater, occasionally epibiotic.

V. patellina Müller, 1776

V. fornicata (Dons, 1915) Noland & Finley, 1931

Diagnosis (Fig. 35b). Zooid 90 µm long × 60 µm wide, conical in shape with no constriction below the wide peristomial lip which measures 90 µm across; disc convex; infundibulum short; macronucleus short, C-shaped and situated longitudinally in centre of zooid; pellicular striations not visible; stalk up to 360 µm long.

Habitat. Marine; forms pseudocolonies.

V. picta Ehrenberg, 1831

V. appunctata (Fromentel, 1874) Noland & Finley, 1931
V. picta var. *major* Nenninger, 1948
V. plicata (Fromentel, 1874) Noland & Finley, 1931

Diagnosis (Fig. 36a). Zooid 41–63 µm long (mean 58 µm) × 20–37 µm wide (mean 32 µm), inverted bell-shaped and slightly constricted beneath peristomial lip which measures 35–50 µm across (mean 45 µm); disc convex; two C.V.'s situated in upper one-third of body; macronucleus long, J-shaped and situated longitudinally in zooid with upper arm lying horizontally across the peristome; pellicle finely striated; stalk

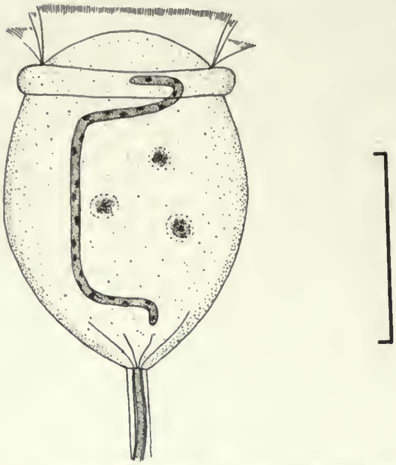

Fig. 37. *V. poznaniensis* (after Piesik, 1976), bar = 50 μm.

4·0–7·0 μm wide (mean 5·9 μm) and up to 550 μm long (mean 340 μm); spasmoneme has row of highly refractile thecoplasmic granules which may be either red or green.

HABITAT. Freshwater; forms pseudocolonies.

V. platysoma Stokes, 1887

DIAGNOSIS (Fig. 36b). Zooid 25 μm long × 15 μm wide, inverted bell-shaped and slightly constricted below peristomial lip which measures 18 μm across; disc flat and obliquely elevated; infundibulum broad and reaches centre of zooid; C.V. situated in upper one-third of body and empties into ventral wall of infundibulum; macronucleus C-shaped and lies transversely across centre of zooid; pellicle distinctly striated and with concave ribbing between striations.

HABITAT. Freshwater; occasionally epibiotic.

REMARKS. Redescribed by Foissner (1979) with biometric analysis.

V. poznaniensis Piesik, 1976

DIAGNOSIS (Fig. 37). Zooid inverted bell-shaped, 68–85 μm long × 62–68 μm wide; constricted beneath peristomial lip the diameter of which is about equal to the maximum body width; disc convex; one c.v.; macronucleus J-shaped and typically very thin; pellicular striations not visible; stalk 7 μm wide.

HABITAT. Freshwater, attached to crayfish and *Cyclops* sp.

V. pulchella Sommer, 1951

DIAGNOSIS (Fig. 38a). Zooid 46 μm long × 30 μm wide, somewhat rotund and constricted beneath peristomial lip which measures 20 μm across; disc narrow and prominently arched above peristome; infundibulum reaches $\frac{3}{4}$ body length; C.V. centrally located and empties into infundibulum; macronucleus short, C-shaped and lies transversely across centre of zooid; pellicle distinctly striated and has convex ribbing between the striations.

HABITAT. Freshwater, originally found as an epibiont attached to the crustacean, *Cyclops* sp.

V. pulchra Kahl, 1933

DIAGNOSIS (Fig. 38b). Zooid 40–50 μm long × 20 μm wide, inverted bell-shaped and strongly constricted below peristomial lip which measures 25 μm across and is furnished with a row of short, pointed projections; disc flat and obliquely elevated above peristome; cilia long and prominent; infundibulum short; C.V. centrally located; macronucleus long, C-shaped and lies longitudinally with respect to major axis of body; pellicle distinctly striated.

HABITAT. Marine.

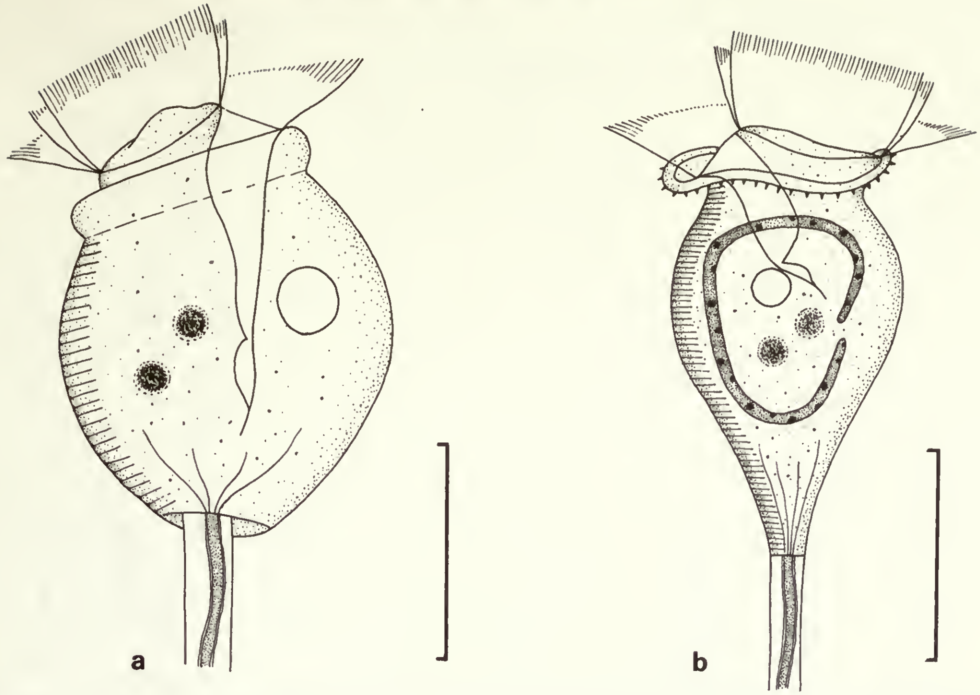

Fig. 38. (a) *V. pulchella* (after Sommer, 1951), bar = 25 µm; (b) *V. pulchra* (after Kahl, 1935), bar = 25 µm.

V. pyriforme Stiller, 1939

V. intermissa Nenninger, 1948

Diagnosis (Fig. 39a). Zooid 45–70 µm long × 30–40 µm wide, inverted bell-shaped with slight constriction beneath peristomial lip which measures 35 µm across; disc flat and slightly elevated; infundibulum broad and reaches centre of zooid; C.V. situated in upper one-third of body; macronucleus C-shaped and lies transversely across centre of zooid; pellicular striations not visible; stalk up to 400 µm long.

Habitat. Freshwater or marine.

V. quadrangularis Kent, 1881

V. sinuata (Zacharias, 1903) Noland & Finley, 1931
V. zealandica (Kirk, 1887) Noland & Finley, 1931

Diagnosis (Fig. 35b). Zooid 200 µm long × 60 µm wide, elongate and with a characteristic constriction in the central region; the body is also constricted beneath the peristomial lip which measures 65 µm across; disc flat and obliquely elevated; C.V. situated beneath peristome; pellicle finely striated; stalk slender and up to 300 µm long.

Habitat. Freshwater ponds, often forming large pseudocolonies.

V. rhabdophora Stokes, 1885

Diagnosis (Fig. 40a). Zooid 80 µm long × 30 µm wide, asymmetrical with one side almost straight while the other has a prominent bulge; disc flat; macronucleus long, J-shaped and situated longitudinally in body with upper arm lying horizontally across peristome; pellicle finely striated and has a mucilagenous covering which contains numerous rod-shape bacteria; stalk up to 160 µm long.

Habitat. Freshwater.

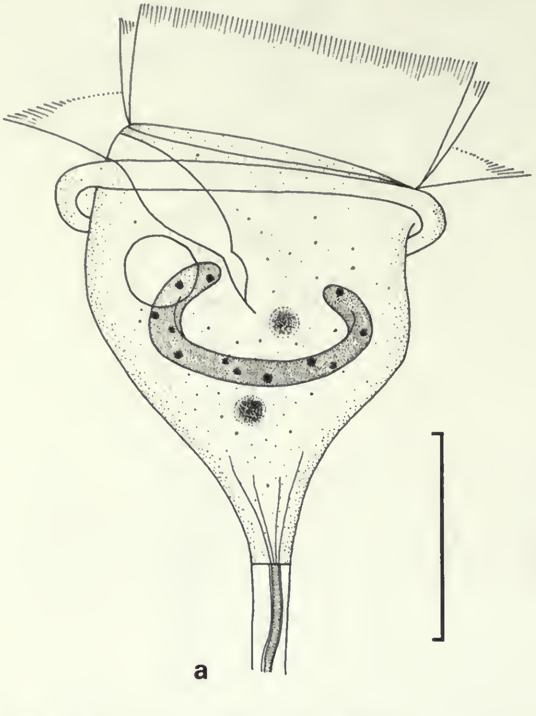

Fig. 39. (a) *V. pyriforme* (after Stiller, 1935), bar = 25 µm; (b) *V. quadrangularis* (after Kent, 1880–82), bar = 50 µm.

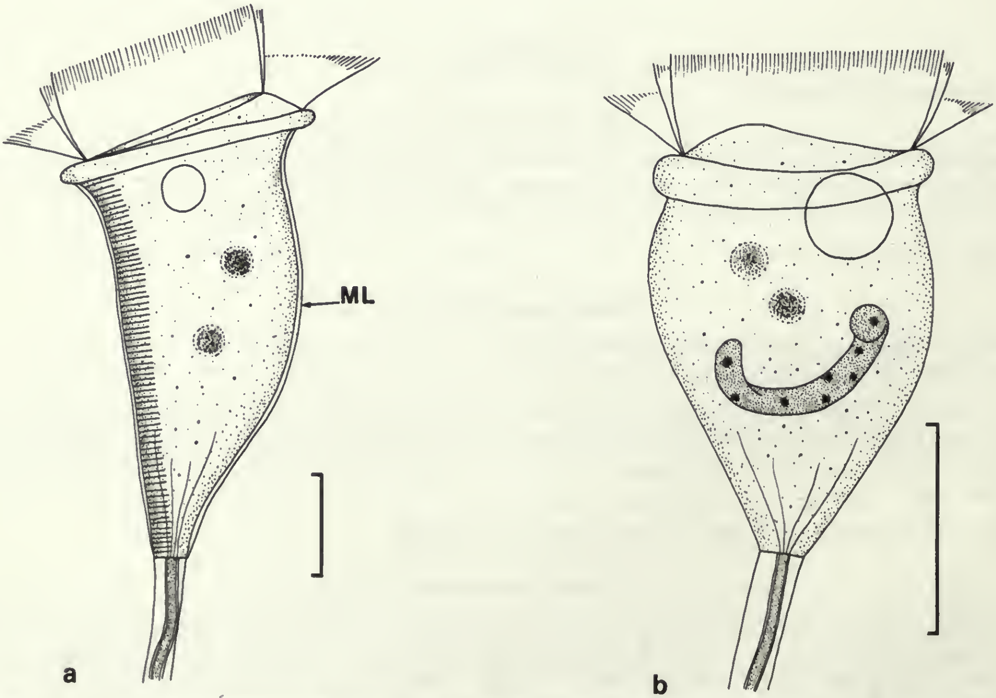

Fig. 40. (a) *V. rhabdophora* (after Stokes, 1885*c*), bar = 25 µm, ML = mucus layer; (b) *V. rotunda* (after Nenninger, 1948), bar = 25 µm.

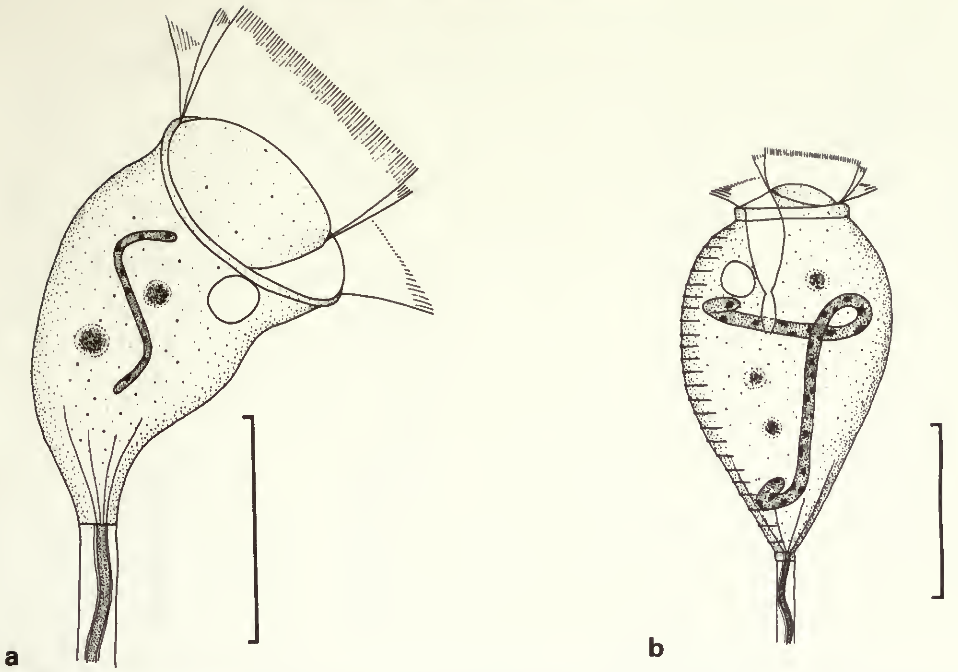

Fig. 41. (a) *V. rubristigma* (after Kellicott, 1888), bar = 25 µm; (b) *V. sepulcreti* (after Foissner & Schiffmann, 1975), bar = 50µm.

V. rotunda Nenninger, 1948

V. octava var. *asellicola* Stiller, 1953

Diagnosis (Fig. 40b). Zooid 49 µm long × 30 µm wide, inverted bell-shaped with slight constriction below peristomial lip which measures 30 µm across; disc convex; C.V. situated in upper one-third of body; macronucleus C-shaped and lies transversely across centre of zooid; pellicular striations not observed.

Habitat. Freshwater, originally found as an epibiont attached to the crustacean *Lestes* sp.

V. rubristigma Kellicott, 1888

Diagnosis (Fig. 41a). Zooid 35 µm long × 20 µm wide, curved and slightly constricted beneath peristomial lip which measures 25 µm across; disc flat and obliquely elevated; C.V. situated just below peristome; macronucleus S-shaped and lies longitudinally in centre of body; pellicular striations not visible; stalk up to 300 µm long; spasmoneme has several rows of red thecoplasmic granules.

Habitat. Freshwater, solitary.

V. sepulcreti Foissner & Schiffmann, 1975

Diagnosis (Fig. 41b). Zooid 45–55 µm long × 25–30 µm wide; disc convex; peristomial lip collar-like and measures 15 µm in diameter; one c.v. situated in upper one-third of zooid close to infundibulum; macronucleus J-shaped; pellicle has a total of 38–43 (mean 40) striations with concave ribbing between striations; stalk up to 500 µm long.

Habitat. Freshwater.

V. striata Dujardin, 1841

V. aquae-dulcis (Stokes, 1887) Noland & Finley, 1931
V. conochili (Stokes, 1889) Noland & Finley, 1931

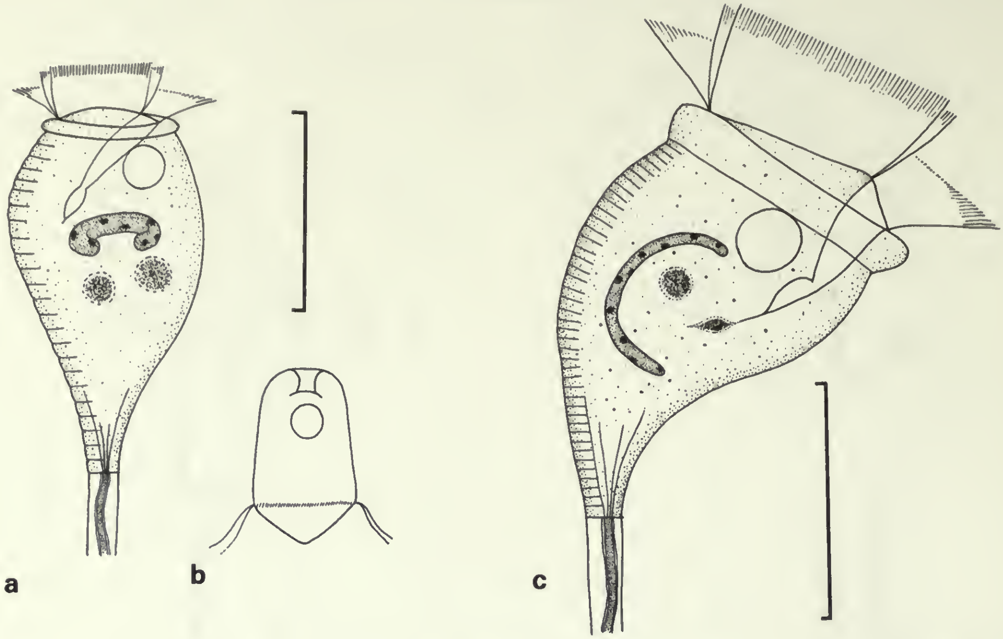

Fig. 42. (a) *V. striata* zooid; (b) telotroch (after Noland & Finley, 1931), bar = 25 µm; (c) *V. subprocumbens* (after Ghosh, 1922), bar = 25 µm.

V. latestriata Sommer, 1951
V. lemnae (Stokes, 1886) Noland & Finley, 1931
V. minima Stiller, 1939
V. oceanica (Zacharias, 1906) Noland & Finley, 1931
V. octava (Stokes, 1885) Noland & Finley, 1931
V. pulsilla (Stokes, 1887) Noland & Finley, 1931
V. pyrum (Mereschkowsky, 1879) Noland & Finley, 1931
V. pyum collaris Wang Jiaji, 1974
V. rhabdostyloides (Kellicott, 1885) Noland & Finley, 1931
V. striata var. *octava* Noland & Finley, 1931
V. striatula (Dons, 1915) Noland & Finley, 1931
V. suboctava Sommer, 1951

DIAGNOSIS (Figs 42a & b). Zooid 20–50 µm long (mean 35 µm) × 15–32 µm wide (mean 19 µm); constricted beneath peristomial lip which measures 13–26 µm across (mean 18 µm); disc convex; C.V. situated just below peristome; macronucleus C-shaped and lies transversely across centre of body; pellicle distinctly striated and with convex ribbing between striations; stalk 1·6–4·0 µm wide (mean 3·0 µm) and up to 300 µm long (mean 100 µm).

HABITAT. Freshwater or marine; solitary; occasionally epibiotic.

V. subprocumbens Ghosh, 1922

V. nana Kahl, 1933
V. solitaria Stiller, 1935

DIAGNOSIS (Fig. 42c). Zooid 30–50 µm long × 20–30 µm wide, asymmetric and curved; slightly constricted below peristomial lip which measures 20–30 µm across; disc flat and obliquely elevated; infundibulum short; C.V. situated in upper one-third of body; macronucleus C-shaped and situated longitudinally with respect to major axis of body; pellicle distinctly striated; stalk up to 150 µm long.

HABITAT. Freshwater or marine; solitary; occasionally epibiotic attached to *Lemna trisulca*.

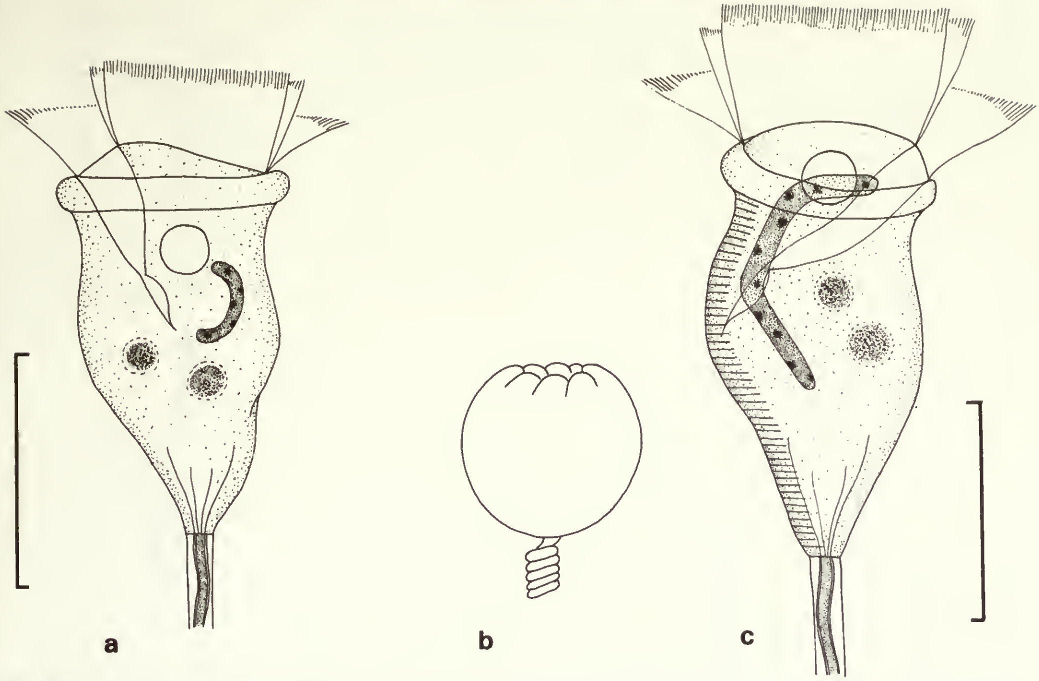

Fig. 43. (a) *V. subsinuata* (after Ghosh, 1922), bar = 25 µm; (b) *V. szczepanowskii*, contracted; (c) *V. szczepanowskii* (after Szczepanowski, 1978), bar = 25 µm.

V. subsinuata Ghosh, 1922

V. longipharyngae Szczepanowski, 1978

Diagnosis (Fig. 43a). Zooid 40–50 µm long × 35–40 µm wide, inverted bell-shaped and may or may not be constricted below peristomial lip which measures 40–45 µm across; infundibulum broad and short; C.V. situated in upper one-third of body; macronucleus short, curved and lies longitudinally in upper $\frac{1}{2}$ of zooid; stalk up to 30 µm long.

Habitat. Freshwater ponds.

V. szczepanowskii (Szczepanowski, 1978) nom. nov.

V. plicata Szczepanowski, 1978

Diagnosis (Fig. 43b). Zooid 43 µm long × 25 µm wide, elongate and constricted beneath peristomial lip which measures 25–30 µm across; disc prominently arched above peristome; macronucleus C-shaped and lies longitudinally in upper $\frac{1}{2}$ of body; pellicle distinctly striated and has convex ribbing.

Habitat. Freshwater, originally found as an epibiont attached to the crustacean *Asellus* sp.

V. telescopica Kent, 1861

V. telescopica var. *marina* Gourret & Roeser, 1886
V. telescopiformis (Gourret & Roeser, 1886) Kahl, 1935

Diagnosis (Fig. 44a & b). Zooid 50 µm long × 15 µm wide, elongate and slightly constricted beneath well developed peristomial lip which measures 15–20 µm across; infundibulum short; C.V. situated in upper one-third of body; macronucleus C-shaped and lies longitudinally in centre of zooid; pellicular striations not visible but there are two characteristic transverse ridges on the pellicle and below each of these, the body becomes abruptly narrower; during contraction, these portions of the zooid overlap; stalk slender and up to 50 µm long.

Habitat. Freshwater or marine; solitary.

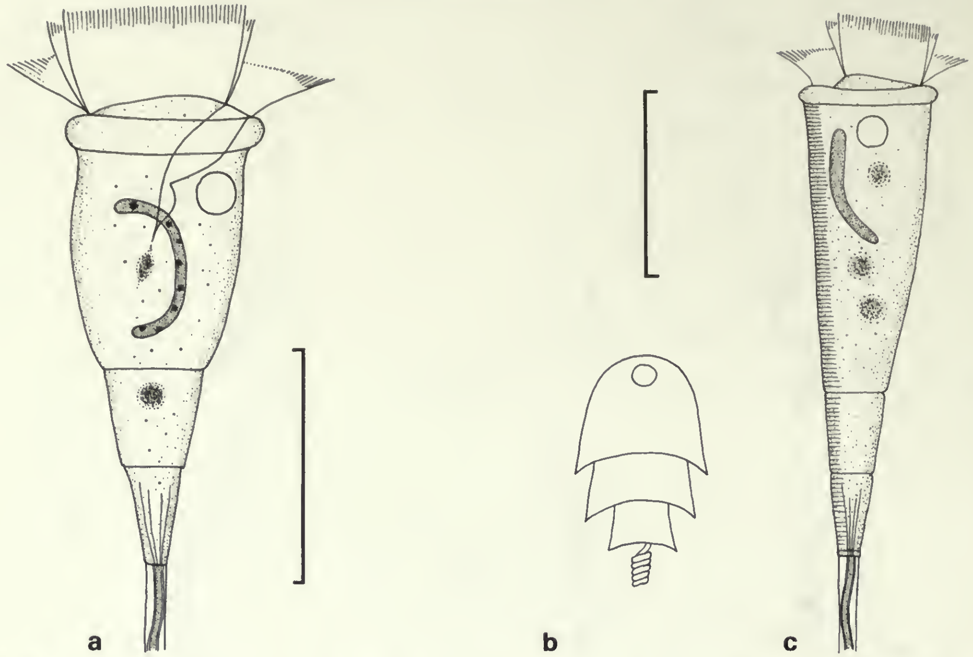

Fig. 44. (a) *V. telescopica* (after Kent, 1880–82), bar = 25 µm; (b) *V. telescopica,* contracted (after Kahl, 1935); (c) *V. telescopoides* (after Šramek-Hušek, 1948), bar = 25 µm.

V. telescopoides (Kahl, 1935) Šramek-Hušek, 1948

V. telescopica Kahl, 1935

Diagnosis (Fig. 44b). Zooid elongate 55–70 µm long × 17–25 µm wide; peristomial lip narrow, 15–20 µm in diameter; disc flat or slightly convex; c.v. situated just beneath peristome; macronucleus short, C-shaped and situated in upper one-third of zooid; pellicle striated; two transverse pellicular ridges are present on lower $\frac{1}{4}$ of zooid and upon contraction the area of the zooid above each overlaps that below.

Habitat. Freshwater.

Remarks. *V. telescopoides* is the name given by Šramek-Hušek (1948*b*) to the animal which Khal (1935) isolated in Hamburg and tentatively identified as ‘*V. telescopia?*’. Šramek-Hušek (1948*b*) redescribed this species from specimens collected from Czechoslovakian rivers.

V. turgicula Wang Jiaji, 1977

Diagnosis (Fig. 45a). Zooid 60–70 µm long × 52–64 µm wide, the middle portion being distinctly swollen; disc dome-shaped and prominently elevated above peristomial lip which measures 32–42 µm in diameter; one c.v. situated just beneath the peristome close to the infundibulum; macronucleus C-shaped and lies transversely across centre of zooid; pellicle faintly striated; stalk 180–315 µm long.

Habitat. Freshwater, originally found attached to aquatic mosses.

V. venusta Nenninger, 1948

V. rotunda var. *asellicola* Stiller, 1953

Diagnosis (Fig. 45b & c). Zooid 36 µm long × 25–30 µm wide, inverted bell-shaped but not constricted beneath peristomial lip which measures 30 µm in diameter; disc convex; c.v. lies in upper one-third of body in the niche formed by the C-shaped macronucleus; pellicle distinctly striated and has convex ribbing between striations; stalk up to 250 µm long; upon contraction the peristomial lip is drawn up in the shape of a narrow cylinder (Fig. 45c).

Habitat. Freshwater, originally isolated as an epibiont on the crustacean *Asellus* sp.

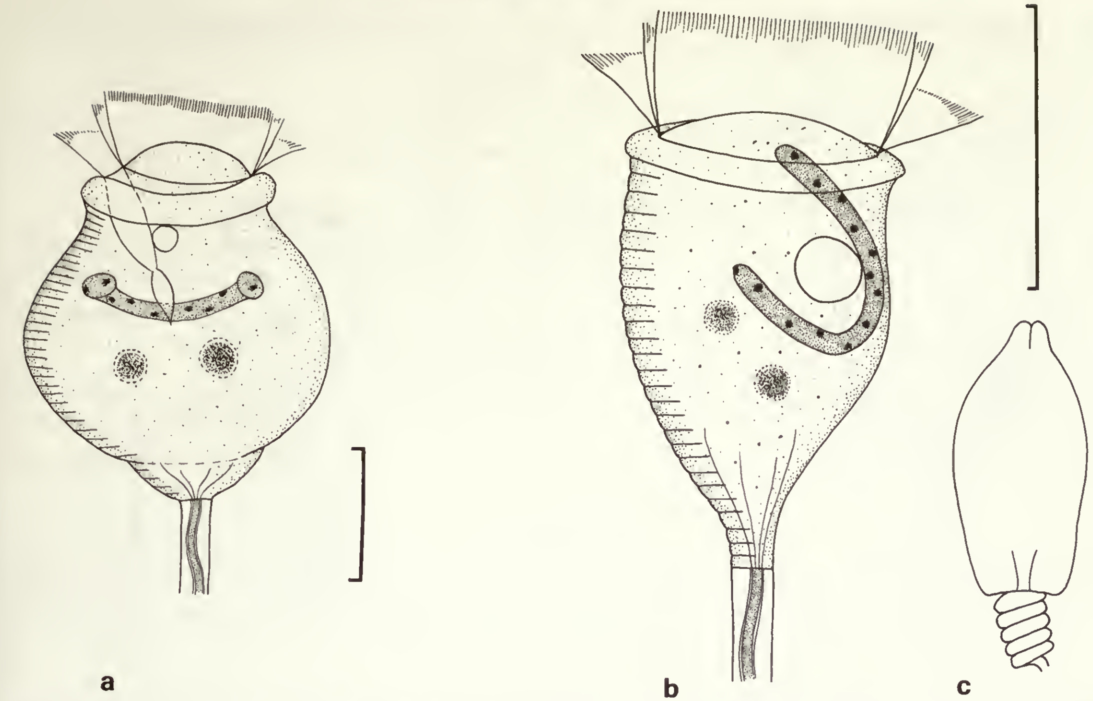

Fig. 45. (a) *V. turgicula* (after Wang Jiaji, 1977), bar = 25 µm; (b) *V. venusta* relaxed zooid; (c) contracted zooid (after Nenninger, 1948), bar = 25 µm.

V. vernalis Stokes, 1887

Diagnosis (Fig. 46a). Zooid 50 µm long × 30 µm wide, elongated trumpet-shaped with no constriction beneath well developed peristomial lip which measures 35 µm across; disc prominently arched above peristome; two C.V.'s situated in upper one-third of zooid; macronucleus long, C-shaped and lies longitudinally with respect to major axis of body; pellicular striations only visible in lower one-third of zooid; pellicle covered with irregularly arranged tubercles and granules; stalk up to 350 µm long.

Habitat. Freshwater ponds.

V. verrucosa Dons (1915), 1918

V. singularis Kahl, 1933

Diagnosis (Fig. 46b). Zooid 60 µm long × 55 µm wide, conical in shape and with no constriction beneath peristomial lip which measures 60 µm across; C.V. situated in upper one-third of body; macronucleus J-shaped with proximal region lying horizontally across peristome; pellicle is furnished with numerous randomly arranged tubercles of various sizes; pellicular striations not visible; stalk 8·0 µm wide and up to 40 µm long.

Habitat. Marine.

V. vestita Stokes, 1883

Pseudovorticella vestita (Stokes, 1883) Jankowski, 1976
V. chlamydophora Penard, 1922

Diagnosis (Fig. 47a). Zooid 50–75 µm long × 40–50 µm wide, inverted bell-shaped and not constricted beneath peristomial lip which measures 55 µm across; disc flat and slightly elevated above peristome; infundibulum reaches two-thirds body length; C.V. situated in upper one-third of zooid; macronucleus

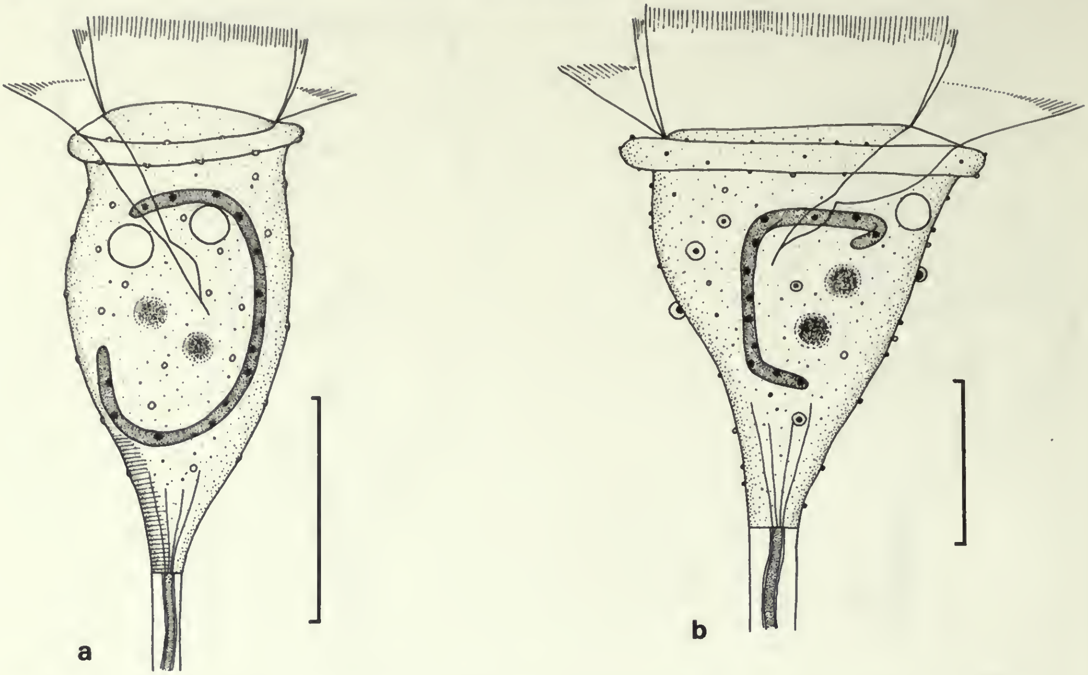

Fig. 46. (a) *V. vernalis* (after Stokes, 1887*b*), bar = 25 µm; (b) *V. verrucosa* (after Küsters, 1974), bar = 25 µm.

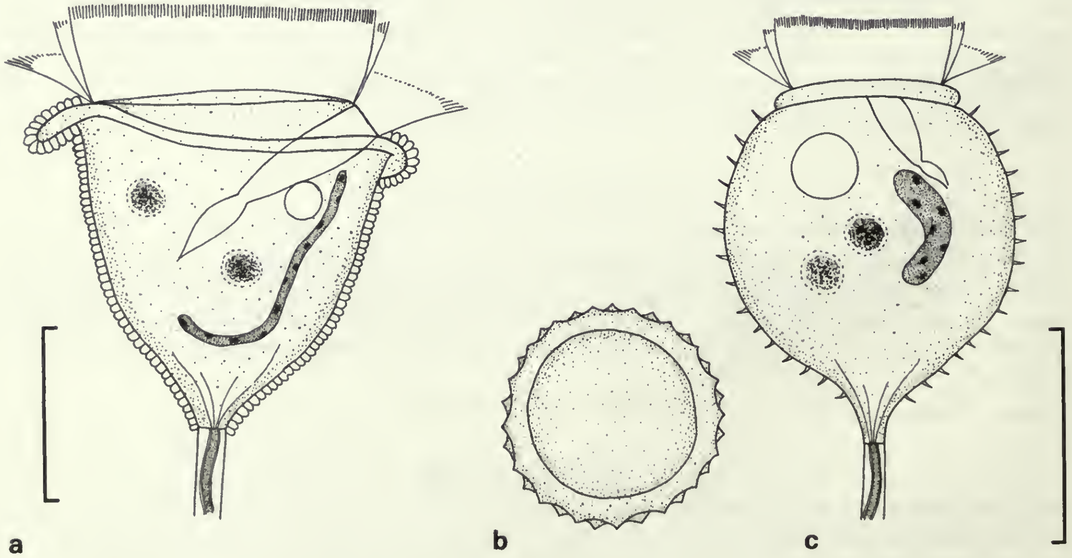

Fig. 47. (a) *V. vestita* (after Stokes, 1883), bar = 25 µm; (b) *V. voeltzkowi* cyst; (c) zooid (after King, 1931), bar = 25 µm.

lies longitudinally with respect to major axis of body; pellicle finely striated; entire zooid covered by transparent, membranous investment which is divided into compartments; stalk up to 400 µm long.

HABITAT. Freshwater, often forming large pseudocolonies.

REMARKS. According to Noland & Finley (1931) *V. vestita* has two C.V.'s but in his original description, Stokes (1883) indicated that only one C.V. is present.

V. voeltzkowi Sondheim, 1929

Pseudovorticella voeltzkowi (Sondheim, 1929) Jankowski, 1976
V. echina King, 1933

DIAGNOSIS (Fig. 47b). Zooid 30–40 µm long × 30–40 µm wide, somewhat rotund, but slightly elongated distally and constricted below peristomial lip which measures 15–20 µm across; disc flat; infundibulum short and broad; C.V. situated in upper one-third of body; macronucleus short, thick, C-shaped and lies longitudinally in centre of zooid; pellicle covered in short, pointed projections, 3·0–4·0 µm long; pellicular striations not visible; stalk up to 140 µm long.

HABITAT. Freshwater.

Addendum

Four new species of *Vorticella* were described by Banina (1983) from activated sludge at the Experimental Aeration Station, Petrodvorets, Old Peterhof, USSR. These are:

V. aerotenci Banina, 1983

DIAGNOSIS Zooid 90–140 µm long × 32–60 µm wide, elongate with upper part cylindrical and lower part rounded; not constricted beneath peristomial lip, the diameter of which is greater than the maximum body width; disc convex; single large c.v. situated in upper one-third of zooid; macronucleus C-shaped and lies longitudinally with respect to major body axis; cytoplasm granular; pellicle finely striated; stalk thick and up to 140 µm long.

V. geispicae Banina, 1983

DIAGNOSIS Zooid 68–122 µm long × 24–48 µm wide, upper part cylindrical and lower part cone-shaped; not constricted beneath peristomial lip, the diameter of which is slightly greater than the maximum body width; two c.v.'s situated in upper part of body; macronucleus slender and elongate with the upper end curved across the peristome and the lower end extending longitudinally down the body; pellicle finely striated; bundles of fibrils conspicuous in lower part of zooid radiating from scopula; stalk somewhat shorter than body length.

V. peterhoffi Banina, 1983

DIAGNOSIS Zooid 62–80 µm long × 35–46 µm wide, inverted bell-shaped and held at an angle on stalk; constricted beneath peristomial lip, the diameter of which is less than the maximum body width; disc slightly convex; infundibulum lies horizontally across upper part of zooid; single c.v. situated just below peristome; macronucleus thick, irregular or dumb-bell shaped and lies either obliquely or longitudinally with respect to major body axis; pellicular striations not observed; stalk length greater than zooid length.

V. hyalina Banina, 1983

DIAGNOSIS Zooid 96–100 µm long × 48–54 µm wide, inverted bell-shaped and constricted beneath peristomial lip, the diameter of which is equal to the maximum body width; disc flat; single c.v. situated in upper one-third of zooid; macronucleus slender and J-shaped; cytoplasm clear and transparent; pellicular striations not observed; stalk slender and several times longer than its body.

Reference

Banina, N. N. 1983. Peritricha Sessilida in activated sludge biocenosis. [in Russian]. *Protozoologiya* **8:** 87–116.

Acknowledgements

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References

Andrussowa, I. 1886. Infusorii Kerchenskoe buxte. *Trudy St. Petersbourg Obshchestva Estestvoispytatalei* **17:** 236–259.

Barausova, O. M. 1983. Morphological variability of infusoria of the genus *Vorticella* in activated sludge [in Russian]. *In:* N. N. Banina, T. V. Beyer & K. M. Sukhanova Eds., *Protozoa of activated sludge,* Series *Protozoology,* no. 8. Academy of Sciences of USSR.

Barlow, B. M. & Finley, H. E. 1976*a*. Comparative studies on four species of *Vorticella* by scanning electron microscopy. *Transactions of the American Microscopical Society* **95:** 352–356.

—— **&**` —— 1976*b*. Comparative studies on four species of *Vorticella* by conventional microscopy. *Transactions of the American Microscopical Society* **95:** 346–351.

Biernacka, I. 1963. Die Protozoenfauna in Danziger Bucht. II. Die Charakteristik der Protozoen in Untersuchten Biotopen der Seekuste. *Polskie Archiwum Hydrobiologii* **11:** 17–75.

Bory de St. Vincent, J. B. 1824. *Essai d'une Classification des Animaux Microscopiques.* 104 pp. Paris.

Brand, T. von 1923. Die Encystierung bei *Vorticella microstoma* und hypotrichen Infusorien. *Archiv für Protistenkunde* **47:** 59–100.

Bussers, J. C. & Jeuniaux, C. 1974. Recherche de la chitine dans les productions métaplasmatiques de quelques Ciliés. *Protistologica* **10:** 43–46.

Carey, P. G. & Warren, A. 1983. The role of surface topography in the taxonomy of peritrich ciliates. *Protistologica* **19:** 73–89.

Corliss, J. O. 1979. *The Ciliated Protozoa: Characterisation, Classification and Guide to the Literature,* 2nd ed. 455 pp. Pergamon Press, Oxford.

—— **& Esser, S. C.** 1974. Comments on the role of the cyst in the life cycle and survival of free-living protozoa. *Transactions of the American Microscopical Society* **93:** 578–593.

Cuénot, L. 1891. Protozoaires commensaux et parasites des echinodermes. *Revue Beligique du Nord de la France* **3:** 292–293.

Curds, C. R. 1969. *An illustrated key to the British freshwater ciliated protozoa commonly found in activated sludge.* Water Pollution Research Technical Paper No. 12. 90 pp. H.M.S.O., London.

——**, Gates, M. A. & Roberts, D. McL.** 1983. *British and Other Freshwater Ciliated Protozoa. Part II Ciliophora: Oligohymenophora and Polymenophora.* 474 pp. Cambridge University Press, Cambridge.

——**, & Vandyke, J. M.** 1966. The feeding habits and growth rates of some fresh-water ciliates found in activated-sludge plants. *Journal of Applied Ecology* **3:** 127–137.

Davidson, A. & Finley, H. E. 1972. A comparative study of argentophilic structures in three peritrich ciliates. *Transactions of the American Microscopical Society* **91:** 8–23.

Dietz, G. 1964. Beiträg zur Kenntnis der Ciliatenfauna einiger Brackwasserstümpel (étangs) der französischen Mittelmeerküste. *Vie et Milieu. Bulletin du Laboratoire Arago, Université de Paris* **15:** 47–93.

Doflein, F. 1901. *Die Protozoen als Parariten und Krankheitserreger, nach biologischen Gesichtspunkten dargestellt.* 274 pp. G. Fischer, Jena.

Dons, C. 1915. Neue marine Ciliaten und Suctorien. *Tromsø Museums Aarshefter* **38:** 75–100.

Dons, C. 1918. Two new vorticellids. *Tromsø Museums Aarshefter* **40:** 1–8.

—— 1922. Notes sur quelques protozaires marins. *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening i Kobenhaun* **73:** 49–84.

Dujardin, F. 1841. *Histoire Naturelle des Zoophytes Infusoires.* 678 pp. Paris.

Ehrenberg, C. G. 1830 (1832). Beiträge zur Kenntnis der Organisation der Infusorien und ihrer Geographischen Verbreitung, besonders in Siberien. *Abhandlungen der Akademie der Wissenchaften der DDR,* year 1832: 1–88.

—— 1831 (1832). Über die Entwicklung und Lebensdauer der Infusionthiere; nebst ferneren Beiträgen zu einer Vergleichung ihrer Organischen Systeme. *Abhandlungen der Akademie der Wissenchaften der DDR,* year 1831: 1–154.

—— 1838. *Die Infusionsthierchen als Volkommene Organismen.* 612 pp. Leipzig.

Fauré-Fremiet, E. 1904. La *Vorticella citrina* et la fonction adipogenique chez les Vorticellinae. *Compte Rendu Hebdomadaire des Séances de l'Académie des Sciences. Paris.* **57:** 390–392.

—— 1920. Sur une nouvelle vorticellide planktonique *Vorticella mayeri. Bulletin de la Societé Zoologique de France* **45:** 103–104.

—— 1924. Contribution à la connaissance des infusoires planktoniques. *Bulletin Biologique de la France et de la Belgique.* Suppl. **6:** 1–171.

—— 1965. The comparative morphology of the Peritrichida ciliates. *In:* Proceedings of the 2nd, International Conference on Protozoology, London, July–August 1965. *Progress in Protozoology,* pp. 13–14.

Finley, H. E. & Lewis, A. C. 1960. Observations on excystment and encystment of *Vorticella microstoma. Journal of Protozoology* **7:** 347–351.

Foissner, W. 1979. Peritrichen Ciliaten (Protozoa: Ciliophora) aus Alpinen Kleingewässern. *Zoologische Jahrbücher (Systematik)* **106:** 529–558.

—— 1981. Morphologie und Taxonomie einiger Heterotricher und Peritricher Ciliaten (Protozoa: Ciliophora) aus Alpinen Böden. *Protistologica* **17:** 29–43.

—— **& Schiffmann, H.** 1974. Vergleichende Studien an argyrophilen Strukturen von vierzehn peritrichen Ciliaten. *Protistologica* **10:** 489–508.

—— & —— 1975. Biometrische und morphologische Untersuchungen über die Variabilität von argyrophilen Strukturen bei peritrichen Ciliaten. *Protistologica* **11:** 415–428.

Fromentel, E. de 1874–1876. *Études sur les Microzoaires ou Infusoires Proprement Dits, Comprenant de Nouvelles Reserches sur Leur Organisation, Leur Classification, et al Description des Espèces Nouvelles ou Peu Connues.* 364 pp. G. Masson, Paris.

Fukui, T. & Morishita, H. 1961. Systematic studies on protozoa found in activated sludge I. *Bulletin of the Yokohama Municipal University Society* **13:** 1–6.

Gajewskaja, N. 1933. Zur Oekologie, Morphologie und Systematik der Infusorien des Baikalsees. *Zoologica, Stuttgart* **32:** 1–298.

Ghosh, E. 1922. New species of *Vorticella* from Calcutta. *Bulletin of the Carmichael Medical College, Belgachia, Calcutta* **3:** 8–18.

Giard, A. 1879. Les Orthonectides, classe nouvelle du phylum des Vermes. *Journal de l'Anatomie et de la Pathologie Normales et Pathologiques de l'Homme et des Animaux, Paris* **15:** 449–464.

Goldfuss, G. A. 1820. *Handbuch der Zoologie.* Vol. 1, Nürnberg.

Gourret, F. & Roeser, P. 1886. Les protozoaires de vieux port de Marseille. *Archives de Zoologie Expérimentale et Générale, Paris* (Series 2) **4:** 443–534.

—— 1888. Contribution à l'études des protozoaires de la Corse. *Archives de Biologie* **8:** 139–204.

Graham, L. E. & Graham, J. M. 1978. Ultrastructure of endosymbiotic *Chlorella* in a *Vorticella. Journal of Protozoology* **25:** 207–210.

—— & —— 1980. Endosymbiotic *Chlorella* (Chlorophyta) in a species of *Vorticella* (Ciliophora). *Transactions of the American Microscopical Society* **99:** 160–166.

Greeff, R. 1870. Untersuchungen über den Bau und die Naturgeschlichte der Vorticellen. *Archiv für Naturgeschichte* **37:** 353–384.

—— 1888. Studien über Protozoen. *Sitzungsberichte der Gesellschaft zu Beförderung der Gesanten Naturwissenschaften zu Marburg* **23:** 90–158.

Green, J. 1974. Parasites and epibionts of Cladocera. *Transactions of the Zoological Society of London* **32:** 417–515.

Guhl, W. 1972. *Opercularia inclinans* (O. F. Müller 1786) nov. comb. ein symphoriontes Peritrich von Oligochaeten. *Zoologischer Anzeiger* **189:** 351–356.

—— 1979. *Opercularia coarctata,* ein variables Peritrich. *Archiv für Protistenkunde* **121:** 308–346.

Hemprich, F. G. & Ehrenberg, C. G. 1828. *Symbolae physicae.* Pars Zool. IV Animalia Envertebrata, Berlin.

Hobbs, E. S. & Lang, H. E. 1964. Observations on argentophilic granules of certain peritrichs. *Journal of Protozoology* **11:** 21–30.

Horikami, H. & Ishii, K. 1981. Cluster inducing factor secreted by *Vorticella* telotroch. *In:* Abstracts of the 6th International Congress on Protozoology, Warsaw. *Progress in Protozoology,* p. 145.

International Code of Zoological Nomenclature, 1964. Adopted by the XV International Congress of Zoology, London, July 1958. 2nd ed., 176 pp.

Jankowski, A. W. 1976. Revision of the order Sessilida (Peritricha) [in Russian]. In: *Material and Public Meeting of Protozoology 1.* Kiev 1976, pp. 168–170.

—— 1980. Conspectus of a new system of the phylum Ciliophora [in Russian]. *Trudy Zoologicheskogo Instituta Leningrad* **94:** 103–121.

Kaas, P. G. 1921 (1920). Communicazione intorno ad una nuova specie di *Vorticella. Atti dell'Accademia Pontificia dei Nuovi Lincei* **74:** 32.

Kahl, A. 1933. Ciliata libera et ectocommensalia. *In:* G. Grimpe & E. Wagler Eds., *Die Tierwelt der Nord- und Ostsee,* Lief. 23 (Teil, II, c_3); Leipzig, pp. 147–183.

—— 1935. Urtiere oder Protozoa. I: Wimpertiere oder Ciliata (Infusoria), eine bearbeitung der freilebenden und ectommensalen Infusorien der Erde, unter Ausschluss der marinen Tintinnidae. 4. Peritricha und Chonotricha. *In:* G. Grimpe & E. Wagler Eds., *Die Tierwelt Deutschlands,* Tiel **30:** 651–864.

Kawamura, R. 1973. The ciliary and fibrillar systems of the ciliate *Vorticella*. *Journal of Science of the Hiroshima University*, Series B: **24:** 183–203.

Keiser, A. 1921. Die Sessilen peritrichen Infusorien und Suktorien von Basel und Umgebung. *Revue Suisse de Zoologie* **28:** 221–341.

Kellicott, D. S. 1885. Observations on some freshwater Infusoria. *Proceedings of the American Society of Microscopists* **8:** 38–47.

—— 1888. Observations on freshwater Infusoria. *Proceedings of the American Society of Microscopists* **10:** 97–106.

Kent, W. S. 1880–82. *A Manual of the Infusoria*. 913 pp. David Brogue, London.

King, R. L. 1933. Two new infusoria (Protozoa) from Iowa. *Proceedings of the Iowa Academy of Sciences* **38:** 241–243.

Kirby, H. 1942. A parasite of the macronucleus of *Vorticella*. *Journal of Parasitology* **28:** 311–314.

Kirk, T. W. 1887. New infusoria from New Zealand. *Annals and Magazine of Natural History* **19:** 439–441.

Klein, B. M. 1926. Ergebnisse mit einer Silbermethode bei Ciliaten. *Archiv für Protistenkunde* **56:** 243–280.

—— 1927. Die Silberlinien system der Ciliaten. *Archiv für Protistenkunde* **58:** 55–142.

Kolkwitz, R. & Marsson, M. 1909. Oekologie der tierischen Saprobien. *Internationale Revue der Gesamten Hydrobiologie* **2:** 126–152.

Küsters, E. 1974. Okologische und systematische Untersuchungen der Aufwuchsciliaten in Königshafen bei List/Sylt. *Archiv für Hydrobiology* (Suppl.) **45:** 121–211.

Lepsi, J. 1948. Protozen aus Boden und Laubstreu eines Eichenwaldes. *Notationes Biologicae, Bucharesti* **6:** 149–159.

—— 1965. *Protozoologie*. 999 pp. Academia Republicii Socialiste Romania.

Levine, N. D., Corliss, J.O., Cox, F. E. G., Deroux, G., Grain, J., Honiberg, B. M., Leedale, G. F., Loeblich, A. R., Lom, J., Lynn, D., Merinfield, E. G., Page, F. C., Poljansky, G., Sprague, V., Vavra, J. & Wallace, F. G. 1980. A newly revised classification of the Protozoa. *Journal of Protozoology* **27:** 37–58.

Linnaeus, C. 1758, 1767. *Systemae Naturae*. Vol. 1: 10th ed., 823 pp. 12th ed., 1327 pp., Salvii, Holmiae.

Lom, J. 1964. The morphology and morphogenesis of the buccal ciliary organelles in some peritrichous ciliates. *Archiv für Protistenkunde* **107:** 131–162.

Mackinnon, D. L. & Hawes, R. L. J. 1961. *An Introduction to the Study of Protozoa*. 506 pp. Oxford University Press.

Mereschkowsky, C. 1877. Studies on the protozoa of northern Russia [in Russian]. *Trudy Sankt Petersburgskoe obshchestvo estestvoispytatelei* **7:** 203–395.

—— 1879. Studen über Protozoen des nordlichen Russlands. *Archiv für Mikroskopische Anatomie* **16:** 153–248.

Müller, O. F. 1773. *Vermium Terrestrium et Fluviatilium, seu Animalium Infusorium, Helminthicorum et Testaceorum, non Marinorum, Succincta Historia* 135 pp. Havniae et Lipsiae.

—— 1776. *Zoologiae Banicae Prodromus, seu Animalium Daniae et Norwegiae Indigenarum Characters, Nomina, et Synonyma Imprimis Popularum*. 282 pp. Havinae.

—— 1786. *Animalcula Infusoria Fluviatilia et Marina*. 367 pp. Havniae et Lipsiae.

Nenninger, U. 1948. Die Peritrichen der Umgebung von Erlangen mit besonderer Berüksichtigung ihrer Wirtsspezifität. *Zoologische Jahrbücher (Systematik)* **77:** 169–266.

Noland, L. E. 1925. Factors influencing the distribution of freshwater ciliates. *Ecology* **6:** 437–452.

—— **& Finley, H. E.** 1931. Studies on the taxonomy of the genus *Vorticella*. *Transactions of the American Microscopical Society* **50:** 81–123.

Penard, E. 1922. *Études sur les Infusoires d'Eau Douce*. 331 pp. George & Cie, Geneva.

Piesik, Z. 1975. Orzeski epizoiczne na kiezach z podrodza ju *Rivulogammarus* Karaman strumieni okolic Poznania. *Badania Fizjograficzne nad Polska Zachodnia, Poznán*. (Zool.) **28:** 41–77.

—— 1976. Przyczynek do znajomosci orzesko epizoicznych (Ciliata–Peritricha) wielkopolski. *Badania Fizjograficzne nad Polska Zachodnia* Ser. C–Zoologia **29:** 151–157.

Pratt, J. R. & Rosen, B. H. 1983. Association of species of *Vorticella* (Peritrichida) and planktonic algae. *Transactions of the American Microscopical Society* **102:** 48–54.

Precht, H. 1935. Epizoen der Kieler Bucht. *Nova Acta Leopoldina* **3:** 405–474.

de Puytorac, P., Batisse, A., Bohatier, J., Corliss, J. O., Deroux, G., Didier, P., Dragesco, J., Fryd-Versavel, G., Grain, J., Grolière, C-A., Hovasse, E., Iftode, F., Laval, M., Roque, M., Savoie, A. & Tuffrau, M. 1974. Proposition d'une classification du phylum Ciliophora Doflein, 1901 (Réunion de Systematique, Clermont-Ferrand). *Compte Rendu Hebdomadaire des Séances de l'Académie des Sciences, Paris* **278:** 2799–2802.

Raabe, Z. 1964. The taxonomic position and rank of Peritricha. *Acta Protozoologica* **2:** 19–32.

Randall, J. T. & Hopkins, I. M. 1962. On the stalks of certain peritrichs. *Philosophical Transactions of the Royal Society of London* **245:** 59–79.

Reid, R. 1967. Morphological studies on three *Vorticella* species. *Transactions of the American Microscopical Society* **86:** 486–493.

Roberts, D. McL., Warren, A. & Curds, C. R. 1983. Morphometric analysis of outline shape applied to the genus *Vorticella. Systematic Zoology* **32:** 377–388.

Schmarda, L. K. 1854. Zur Naturgeschichte Ägyptens. *Denkschriften der Kaiserlichen Akademie der Wissenschaften* **7:** 1–28.

Schrank, Fr. P. 1803. *Fauna Boica*. Vol. 3. 184 pp. Nürnberg.

Siebold, C. T. von 1848. Lehrbuch der Vergleichenden Anatomie der Wirbellosen Thiere. *In:* C. T. von Siebold & H. Stannius, *Lehrbuch der Vergleichenden Anatomie* Vol. 1, 679 pp. Berlin.

Sládećek, V. 1971. Saprobic sequences within the genus *Vorticella. Water Research* **5:** 1135–1140.

Sládećková, A. 1962. Limnological investigation methods for the periphyton ("Aufwuchs") community. *Botanical Review* **28:** 286–350.

Small, E. B. & Ranganathan, V. S. 1970. The direct study of polluted stream ciliated protozoa via scanning electron microscopy. *In:* Proceedings of the 3rd Annual Scanning Electron Microscope Symposium, Chicago, April 1970. *Scanning Electron Microscopy*, pp. 177–184.

Sommer, G. 1951. Die Peritrichen Ciliaten des Grossen Plöner Sees. *Archiv für Hydrobiologie* **44:** 349–440.

Sondheim, M. 1929. Protozoen aus der Voeltzkowschen Reisen in Madagaskar und Ostafrika. *Abhandlungen hrsg. von der Senckenbergischen Naturforschenden Gesellschaft* **41:** 285–313.

Spoon, D. M. 1974. Behaviour of telotrochs and microconjugants of sessile peritrichs. *Journal of Protozoology* **21:** 84 (Suppl.).

—— 1975. *Survey, ecology and systematics of the upper Potomac estuary biota; aufwuchs microfauna. Phase I*. Final Report. Water Resources Research Centre, Washington Technical Institute, Washington D.C. 117 pp.

Šramek-Hušek, R. 1946. K Poznáni epizoických nálevniku z řeky Vlatvy. *Věstnik Československé zoologické Spolěcnosii* **10:** 241–244.

—— 1948*a*. K Poznáni planktonou a epizoonu středočeských rybnikú. *Casopis Národniho Musea* **117:** 67–81.

—— 1948*b*. Ciliata-Peritricha našich řek (Přispěvky k poznáni cekeslovenských nálevniků III). *Caposis Náodniho Musea* **117:** 167–183.

Stein, F. von 1859. *Der Organismus der Infusionsthiere nach eigenen Forschungen in systematischer Reihenfolge bearheitet*. I. 206 pp. Leipzig.

Stiller, J. 1931. Die Peritrichen Infusorien von Tihany und Umgebung. *Arbeiten des Ungarischen Biologischen Forschungs Institutes* **4:** 171–205.

—— 1935. Peritrichen der Gewässer des Berges Lázhegy in Ungarn. *Acta Biologica, Szeged* **3:** 145–148.

—— 1938. Neuere Beiträge zur Kenntnis der Peritrichenfauna des Teiches Belsö-Tó Bei Tihany. *Arbeiten des Ungarischen Biologischen Forschungs Institutes* **10:** 247–253.

—— 1939. Die Peritrichenfauna der Nordsee Bei Helgoland. *Archiv für Protistenkunde* **92:** 413–452.

——1940. Beiträge zur Peritrichenfauna des Groben Plöner Sees in Holstein. *Archiv für Hydrobiologie* **36:** 263–285.

—— 1941. Einige Gewässer der Umgebung von Szeged und ihrer Peritrichenfauna. *Archiv für Hydrobiologie* **38:** 313–435.

—— 1946. Beiträge zur Kenntnis der Peritrichenfauna der Adria bei Split. *Annales Historico–Naturales Musei Nationalis Hungarici* **39:** 59–74.

—— 1953*a*. Epizoische Peritrichen aus dem Balaton III. *Hydrobiologia* **5:** 189–221.

—— 1953*b*. Die Protozoen des Pécsely—Baches in Ungarn. *Annales Historico–Naturales Musei Nationales Hungarici* **44:** 47–70.

——1963. Zur Limnologie der Natrongewässer Ungarns. I. Der Natronsee Nagyszék und seine Peritrichenfauna. *Internationale Revue der Gesamten Hydrobiologie und Hydrographie* **48:** 603–612.

—— 1968. Peritriche Ciliaten ökologisch verschiedener Biotope von Rovinj und Umgebung. *Acta Zoologica Academiae Scientiarum Hungaricae* **14:** 185–211.

—— 1971. Szajoszorús Csillósok—Peritricha. *Fauna Hungariae* **105:** 1–245.

Stokes, A. C. 1883. A new *Vorticella. American Monthly Microscopical Journal* **4:** 208.

—— 1884. A new infusorian belonging to the genus *Vorticella. American Naturalist* **18:** 829–830.

—— 1885*a*. Key to vorticellae. *Microscope, Detroit* **5:** 97–101.

—— 1885*b*. Some apparently undescribed infusoria from freshwater. *American Naturalist* **19:** 18–27.

—— 1885*c*. A new *Vorticella. Microscope, Detroit* **5:** 34–36.

—— 1885*d*. On some new infusoria from American freshwaters. *Annals of Natural History* Series 5 **15:** 437–449.

—— 1885*e*. *Vorticella limnetis* (sp. nov.) *Microscope, Detroit* **5:** 145–146.

—— 1886*a*. Notices of new freshwater infusoria. *American Monthly Microscopical Journal* **7:** 81–86.

—— 1886*b*. Some new infusoria from American freshwaters. *Annals and Magazine of Natural History*, Series B **17:** 98–112.

—— 1887*a*. Notices of new freshwater infusoria. *Proceedings of the American Philosophical Society* **24:** 244–255.

—— 1887*b*. Notices of new freshwater infusoria. *American Monthly Microscopical Journal* **7:** 141–147.

—— 1889. Notices of new peritrichous infusoria from the freshwaters of the United States. *Journal of the Royal Microscopical Society* **12:** 477–482.

Szczepanowski, P. 1978. Orzeski epizoiczne na *Asellus aquaticus* (L) Poznania I okolic. *Prac Komisji Matematyczno- Przyrodniczej Poznańskie Towarszystwo Pryjacio Nank Poznań* **46:** 1–72.

Tai, L. S. 1931. Notes on freshwater protozoa of Peiping. *Science Reports of the National Tsing Hua University, Peiping* Series B **1:** 1–60.

Tatem, J. G. 1870. A contribution to the teratology of the infusoria. *Monthly Microscopical Journal* **3:** 194–195.

Taylor, W. D. 1983. A comparative study of the sessile, filter-feeding ciliates of several small streams. *Hydrobiologia* **98:** 125–133.

Tucolesco, J. 1962. Études protozoologiques sur les eaux Roumaines. I. Espèces nouvelles d'infusoires de la Mer Noire et des basins sales paramins. *Archiv für Protistenkunde* **106:** 1–36.

d'Udekem, G. 1864. Descriptions des infusoires de la Belgique *Mémoires de l'Académie Royale des Sciences, des Lettres et des Beaux-Arts de Belgique* **34:** 1–34.

Vavra, J. 1961. Some results of the research of symphoriont ciliates (Peritrichida-Sessilina) of crustaceans in Czechoslovakia. *In:* Proceedings of the 1st International Congress on Protozoology, Prague, August 22–31, 1961. *Progress in Protozoology*, p. 89.

Viljoen, S. & As, J. G. van 1983. A taxonomic study of sessile peritrichians with notes on their substrate preferences. *Journal of the Limnological Society of South Africa* **9**(1): 33–42.

Wang, Jiaji 1974. Report of the scientific investigations on the biology and physiology of a high mountain area of the Jn-moo-long-ma mountain district, 1966–68 [in Chinese]. *China Institute of Science Tibetan Investigation Team*, pp. 166–174.

—— 1977. Protozoa from some districts of Tibetan plateau [in Chinese]. *Acta Zoologica Sinica* **23:** 131–160.

Zacharias, O. 1903. Zur Kenntnis die nierden Flora und Fauna holsteinischer Moorümpfe. *Forschungsberichte aus der Biologischen Station zu Plön* **10:** 239–240.

—— 1906. Über Periodizität, Variation und Verbreitung verschiedener Planktonwesen in südlichen Meeren. *Archiv für Hydrobiology* **1:** 498–575.

Zimmerman, P. 1961. Experimentelle Untersuchungen über die ökologische Wirkung der Strömungsgeschwindigkeit auf die Lebensgemeinschaften des fliessenden Wassers. *Schweizerische Zeitschrift für Hydrobiologie* **23:** 1–81.

Appendix 1

Index of extant species; annotated list of nominal species.

The following list is composed of those species which were not rejected by Noland & Finley (1931) together with the 113 species and varieties described since. *Haplocaulis* Precht, 1935 and *Pseudovorticella* Foissner & Schiffmann, 1974, two genera which closely resemble *Vorticella*, have been erected since Noland & Finley's review and many species previously belonging to *Vorticella* have been transferred to these two. Instances of synonymy, homonymy and the rejection of taxa due to a lack of sufficient information are also indicated.

V. abbreviata (Keiser, 1921) Kahl, 1935 was regarded as a distinct species by both Kahl (1935), and Foissner & Schiffmann (1974), but is considered here to be a variant of *V. infusionum*.

V. aequilata Kahl 1935 (p. 11).

V. alba Fromentel, 1874 was erroneously moved to the genus *Haplocaulis* by Stiller (1971). It appears to be a valid species of *Vorticella* (p. 11).

V. aldabrandina Kaas, 1921 was so poorly figured and described that it cannot be recognised as a distinct species. It therefore is considered to be a *nomen dubium*.

V. alpestris Foissner, 1979 (p. 11).

V. amphitricha Schmarda, 1854 was described from a specimen in the process of telotroch formation. In the absence of a detailed description of a normal vegetative cell, it is now considered to be a *nomen dubium*.

V. amphiurae Cuénot, 1891 was described as having a straight spasmoneme which does not coil up in spiral fashion when it contracts. It should be therefore transferred to the genus *Haplocaulis*

V. anabaenae Stiller, 1940 was transferred to the genus *Haplocaulis* by Stiller (1971).

V. annulata (Gourret & Roeser, 1888) Kahl, 1935 was originally thought to be a variant of *V. brevistyla* but was elevated to the rank of species by Kahl (1935) (p. 13).

V. anomala Gourret & Roeser, 1886 (p. 13).

V. aperta Fromentel, 1874 (p. 13).

V. artemiae Lepsi, 1965. No diagram was given with this poorly described freshwater form which now becomes a *nomen dubium*.

V. astyliformis Foissner, 1981 (p. 13).

V. banatica Lepsi. The original reference could not be located but Stiller (1971) gives a detailed description and diagram of what appears to be a valid species (p. 14).

V. bidulphae Stiller, 1939 (p. 14).

V. bivacuolata Fukui & Morishita, 1961 (p. 14).

V. bosminae Šramek-Hušek, 1948 (p. 15).

V. brevistyla d'Udekem, 1864 was transferred to the genus *Pseudocarchesium* by Stiller (1971).

V. calciformis Kahl, 1933 (p. 15).

V. campanula Ehrenberg, 1831 (p. 15).

V. campanula f. *monilata* Stiller, 1963 has on its pellicle rows of regularly arranged tubercles and is therefore transferred to the genus *Pseudovorticella*.

V. campanula f. *minor* Stiller, 1953 is an epizooic variant of *V. campanula* and is not sufficiently distinct to be known by a separate name.

V. campanula f. *citrina* var. *minor* Stiller, 1953 = *V. campanula*.

V. campanulata (Kahl, 1933), Šramek-Hušek, 1948. This species was redescribed and renamed by Šramek-Hušek (1948) (p. 17).

V. carinogammari Stiller, 1953. Although redescribed by Piesik (1975) under that name it had already been transferred to the genus *Haplocaulis* by Stiller (1971).

V. chinensis Tai, 1931 strongly resembles *V. convallaria* but may be distinguished by its spheroidal macronucleus. However, Kirby (1942) has shown that *Vorticella* macronuclei also typically assume a round-oval shape if parasitised by bacteria. Therefore *V. chinensis* is considered to be a parasitised *V. convallaria*.

V. chlamydophora Penard, 1922 appears to be identical to *V. vestita* Stokes, 1883.

V. chlorellata Stiller, 1940 = *V. chlorostigma* Ehrenberg, 1831.

V. chlorostigma Ehrenberg, 1831 (p. 18).

V. chydoricola Šramek-Hušek, 1946 is an epizooic variant of *V. microstoma*.

V. citrina Müller, 1773 is, according to Fauré-Fremiet (1904), a physiological variant of *V. convallaria*.

V. citrina var. *turgescens* Stiller, 1931 = *V. convallaria*.

V. claparedei Andrussowa, 1886. The mode of contraction of this species suggests that it should be transferred to the genus *Haplocaulis*.

V. claudicans Penard, 1922 was transferred to the genus *Haplocaulis* by Stiller (1971).

V. coeni Lepsi, 1948 was so poorly figured and described that it cannot be recognised as a valid species. It therefore becomes a *nomen dubium*.

V. colorata Mereschkowsky, 1877 was distinguished on the basis of its pink cytoplasm but, according to Noland & Finley (1931), colour alone is insufficient for the separation of species. In the absence of other distinguishing features this species is now considered to be a *nomen dubium*.

V. communis Fromentel, 1874 (p. 18).

V. conica Dons, 1915. Kahl (1935) renamed this species *V. obconica* in order to solve the problem of homonymy with Stoke's (1887*b*) *V. conica*.

V. conosoma Stokes, 1889 was described by Gajewskaja (1933) who indicated that the spasmoneme is straight and that upon contraction the stalk folds rather than coils. Therefore this species is transferred to the genus *Haplocaulis*.

V. constricta Fromentel, 1874 = *V. microstoma*.

V. constricta Kahl, 1933 = *V. campanulata*.

V. constricta Gajewskaja, 1933 is clearly not a *Vorticella* since it forms colonies. Therefore, this species is transferred to the genus *Zoothamnium* and in order to prevent synonymy with *Z. constricta* it is renamed *Zoothamnium gajewskajum* nom. nov.

V. convallaria Linnaeus, 1758 (p. 18).

V. convallaria var. *compacta* Nenninger, 1948 is an epizooic form which only differs from *V. convallaria* by the arrangement of its food vacuoles. This feature was rejected by Noland & Finley (1931) as a basis for separating species.

V. costata (Sommer, 1951) Foissner, 1979 was originally thought to be a variety of *V. octava* but biometric studies by Foissner (1979) have shown that it is a distinct species (p. 19).

V. crassicaulis Kent, 1881 was transferred to the genus *Paravorticella* by Kahl (1935), and subsequently to the genus *Haplocaulis* by Stiller (1971).

V. crassicaulis Nenninger, 1948 appears to be identical to *V. longifilum* Kent, 1881. Synonymising these two also solves the problem of homonymy with the previous species.

V. cratera Kent, 1881 is the name which Kent applied to Ehrenberg's (1838) *V. patellina*. However, Kent's animal is quite unlike any other species of *Vorticella* and *V. cratera* is now designated as a distinct species (p. 20).

V. cupifera Kahl, 1935 appears to be identical to *V. microstoma*. Pratt & Rosen (1983) have also remarked on the similarity of these two species.

V. cyclopicola Kahl, 1935 is probably an epibiotic variety of *V. microstoma*.

V. cyclopis Kahl, 1933 is a marine form which closely resembles *V. convallaria*.

V. cylindrica Dons, 1915 appears to be a marine variety of *V. campanula*.

V. delicatulata Biernacka, 1963 is probably a marine variety of *V. hamata*.

V. difficilis Kahl, 1933 was transferred to the genus *Pseudovorticella* by Jankowski (1976).

V. dimorpha Stiller, 1940 (p. 20).

V. dipneumon Penard, 1922 was transferred to the genus *Haplocaulis* by Stiller (1971).

V. dubia Fromentel, 1874 was so poorly described and figured that it cannot be recognised as a distinct species. It therefore becomes a *nomen dubium*.

V. dudekemi Kahl, 1933 = *V. cratera*.

V. echina King, 1933 = *V. voeltzkowi* Sondheim, 1929.

V. eforiana Tucolesco, 1962. In the original diagram this species is shown as having a short, straight spasmoneme. It should therefore be transferred to the genus *Haplocaulis*.

V. elegans Dons, 1915 was transferred to the genus *Intranstylum* by Nenninger (1948), and later to the genus *Haplocaulis* by Stiller (1971).

V. elongata Fromentel, 1874 (p. 20).

V. ephemerae Kahl, 1935 is an epizooic form which closely resembles *V. convallaria*.

V. epizoica Šramek-Hušek, 1948 was transferred to the genus *Haplocaulis* by Stiller (1971).

V. exilis Nenninger, 1948 (p. 21).

V. extensa Kahl, 1935 was transferred to the genus *Haplocaulis* by Sommer (1951).

V. extensa var. *macronucleata* Nenninger, 1948 was transferred to the genus *Haplocaulis* by Stiller (1971).

V. fasciculata Müller, 1773 is distinguished principally on the basis of its green colouration, a character rejected by Noland & Finley (1931) for the separation of vorticellae. This is now considered to be a *nomen dubium*.

V. flexuosa Nenninger, 1948 (p. 21).

V. fluvialis Fromentel, 1874 is a morphological variant of *V. microstoma*.

V. floridensis Stokes, 1886 closely resembles and is probably synonymous with *V. kenti* (Kent, 1881) Kahl, 1935.

V. fromenteli Kahl, 1935 (p. 21).

V. fusca Precht, 1935 (p. 22).

V. fusca Biernacka, 1963. This species has a short, straight spasmoneme and should therefore belong to the genus *Haplocaulis*. This also solves the problem of homonymy with the previous species.

V. fusiforma Nenninger, 1948 was transferred to the genus *Haplocaulis* by Sommer (1951).

V. globosa Ghosh, 1922 (p. 22).

V. globularia Müller, 1773 (p. 22).

V. gracilis Dujardin, 1841 (p. 23).

V. granulata Kahl, 1933 (p. 23).

V. halophila Stiller, 1941 (p. 23).

V. hamata Ehrenberg, 1831 (p. 25).

V. hyalina Stiller, 1940 closely resembles and is probably synonymous with *V. convallaria.*

V. hyalina Stiller, 1968 was transferred to the genus *Zoothamnium* by Stiller (1971) which also solves the problem of homonymy with the previous species.

V. incerta Nenninger, 1948 is here synonymised with *V. ovum* Dons, 1918.

V. incisa Stiller, 1938 (p. 25).

V. inclinans Müller, 1786 was transferred to the genus *Opercularia* by Guhl (1972).

V. inconstantans Green, 1974 is variable in shape but when fully extended, closely resembles *V. lichenicola.*

V. iners Schrank, 1803 is so poorly described and figured that it is now considered to be a *nomen dubium.*

V. infusionum Dujardin, 1841 (p. 25).

V. intermissa Nenninger, 1948. The main distinguishing feature of this species is the spasmoneme which is incomplete, terminating a short distance below the zooid. However, this character is not accepted for separating species of *Vorticella.* In other respects *V. intermissa* closely resembles *V. pyriforme* Stiller, 1939 with which it is here synonymised.

V. jaerae Precht, 1935 (p. 26).

V. kahli Stiller, 1931 was transferred to the genus *Haplocaulis* by Sommer (1951).

V. kenti (Kent, 1881) Kahl, 1935 (p. 26).

V. latestriata Sommer, 1951 is a morphological variant of *V. striata* Dujardin, 1941.

V. latifunda Nenninger, 1948 (p. 26).

V. lichenicola Greeff, 1888 (p. 27).

V. lima Kahl, 1935 (p. 27).

V. limnetis Stokes, 1885 (p. 27).

V. lockwoodi Stokes, 1884 was synonymised with *V. margaritata* var. *chlorelligera* by Kahl (1935) which has since been transferred to the genus *Pseudovorticella* by Foissner & Schiffmann (1975).

V. longifilum Kent, 1881 (p. 29).

V. longifilum f. *epizooicum* Szczepanowski, 1978 is an epizooite which is not sufficiently distinct to be recognised as a separate taxon.

V. longimacronucleata Fukui & Morishita, 1961 = *V. microstoma* Ehrenberg, 1830.

V. longipharyngea Szczepanowski, 1978 closely resembles *V. subsinuata* Ghosh, 1922.

V. longiseta Dietz, 1964 (p. 29).

V. logitricha Gajewskaja, 1933 (p. 29).

V. lutea Stiller, 1938 (p. 30).

V. lymnaearum Viljoen & As, 1983 (p. 30).

V. macrocaulis Stokes, 1885 = *V. longifilum.*

V. macrophya Stokes, 1885 (p. 30).

V. macrostoma Schmarda, 1854 = *V. campanula.*

V. macrostyla Schmarda, 1854 (p. 30).

V. magna Fukui & Morishita, 1961 = *V. microstoma* Ehrenberg, 1830.

V. margaritata Fromentel, 1874 was transferred to the genus *Pseudovorticella* by Jankowski (1976).

V. margaritata var. *chlorelligera* Kahl, 1935 was transferred to the genus *Pseudovorticella* by Foissner & Schiffmann (1975).

V. marginata Stiller, 1931 (p. 31).

V. marginata f. *poliensis* Stiller, 1931 is, according to Szczepanowski (1978), an ecological variant of *V. marginata* which cannot be recognised as a separate taxon.

V. marginata f. *minor* Stiller, 1931 = *V. marginata* (Szczepanowski, 1978).

V. marina Greeff, 1870 (p. 31).

V. mayeri Fauré-Fremiet, 1920 (p. 31).

V. micata Kahl, 1933 has rows of regularly arranged pellicular tubercles and therefore belongs to the genus *Pseudovorticella.*

V. microscopica Fromentel, 1874 (p. 33).

V. microstoma Ehrenberg, 1830 (p. 33).

V. microstoma var. *defluviatilis* Nenninger, 1948 is a morphological variant of *V. microstoma.*

V. microstoma f. *elongata* Stiller (drawing and description in Stiller, 1971) = *V. microstoma.*

V. microstoma f. *monilata* Stiller (drawing and description in Stiller, 1971) was transferred to the genus *Pseudovorticella* and renamed *P. papillata* by Jankowski (1976).

V. microstoma f. *turgescens* Stiller (drawing and description in Stiller, 1971) = *V. microstroma.*

V. minima Stiller, 1939 is probably an epizooic variety of *V. striata* Dujardin, 1841.

V. minuta Precht, 1935 = *V. marina* Greeff, 1870.

V. molesta Stokes, 1889. In the original description this species was not figured and was so poorly characterised that it cannot be recognised as a distinct species. It therefore becomes a *nomen dubium*.
V. mollis Stokes, 1887 has rows of regularly arranged pellicular tubercles and is therefore transferred to the genus *Pseudovorticella*.
V. monilata Tatem, 1870 was transferred to the genus *Pseudovorticella* by Foissner & Schiffmann (1974).
V. mortensi Dons, 1922 was described from fixed material and is therefore considered to be a *nomen dubium*.
V. muralis Penard, 1922 (p. 34).
V. mutans Penard, 1922 was transferred to the genus *Pseudovorticella* by Foissner (1979).

V. nana Kahl, 1933 is probably a marine variety of *V. subprocumbens* Ghosh, 1922.
V. natans (Fauré-Fremiet, 1924) Kahl, 1935 (p. 34).
V. nebulifera Müller, 1773 was transferred to the genus *Pseudovorticella* by Jankowski (1976).
V. nutans Muller, 1773 (p. 34).

V. obconica (Dons, 1915) Kahl, 1935 (p. 35).
V. oblonga Kirk, 1887 was not figured and only poorly described by the original author. It is therefore considered to be a *nomen dubium*.
V. oceanica Zacharias, 1906 = *V. striata*.
V. octava Stokes, 1885 is a freshwater variety of *V. striata*.
V. octava var. *asellicola* Stiller, 1953 has an unstriated pellicle and is clearly not a variety of *V. octava*. However, it closely resembles, and may be synonymous with, *V. rotunda* Nenninger, 1948.
V. octava f. *costata* Sommer, 1951 was redescribed by Foissner (1979) who elevated it to the rank of species as *V. costata*.
V. operculariformis Foissner, 1979 (p. 35).
V. ophiocomae Giard, 1879. In the original description this species was not figured and was so poorly characterised that it cannot be recognised as a distinct species. It is now considered to be a *nomen dubium*.
V. ovum Dons, 1918 (p. 35).

V. parasita Stokes, 1887 (p. 37).
V. partita Fukui & Morishita, 1961 = *V. microstoma*.
V. patellina Müller, 1776 (p. 37).
V. patellina Ehrenberg, 1838 is a freshwater species which is clearly different from Müller's (1776) *V. patellina*. Noland & Finley (1931) considered this to be a shallow variety of *V. campanula*.
V. pelagica Gajewskaja, 1933 was transferred to the genus *Haplocaulis* by Stiller (1971).
V. perlata Kahl, 1933 = *V. punctata* Dons, 1918.
V. picta Ehrenberg, 1838 (p. 37).
V. pileolata Lepsi, 1948 = *V. microstoma*.
V. platysoma Stokes, 1887 (p. 38).
V. plicata Gourret & Roeser, 1886 is probably a marine variety of *V. elongata*.
V. plicata Szczepanowski, 1978 is a freshwater epizooite and is clearly different from Gourret & Roeser's (1886) *V. plicata*. In order to solve the problem of homonymy, this species is renamed *V. szczepanowskii* nom. nov.
V. poznaniensis Piesik, 1976 (p. 38).
V. procera Nenninger, 1948 was transferred to the genus *Haplocaulis* by Stiller (1971).
V. pulchella Sommer, 1951 (p. 38).
V. pulchra Kahl, 1933 (p. 38).
V. punctata Dons, 1918 has rows of regularly arranged pellicular tubercles and should therefore be transferred to the genus *Pseudovorticella*.
V. putrina Müller, 1776 is not a *Vorticella* as it possesses a rigid, non-contractile stalk. It is therefore transferred to the genus *Rhabdostyla* and becomes *Rhabdostyla putrina* comb. nov.
V. pyriforme Stiller, 1939 (p.39).
V. pyrum collaris Wang Jiaji, 1974 = *V. striata*.

V. quadrangularis Kent, 1881 (p. 39).

V. rhabdophora Stokes, 1885 (p. 39).
V. robusta Dons, 1922 was described from contracted specimens and until healthy, uncontracted cells have been observed this cannot be recognised as a valid species. It therefore becomes a *nomen dubium*.
V. rotunda Nenninger, 1948 (p. 41).
V. rotunda var. *asellicola* Stiller, 1953 = *V. rotunda*.
V. rubristigma Kellicott, 1888 (p. 41).

V. salina Stokes, 1887 was considered by Noland & Finley (1931) to be a freshwater variety of *V. nebulifera* (= *V. convallaria* according to Reid, 1967).
V. sepulcreti Foissner & Schiffmann, 1975 (p. 41).
V. similis Stokes, 1887 was considered by Noland & Finley (1931) to be a freshwater variety of *V. nebulifera*. Reid (1967) has now shown that *V. nebulifera* var. *similis* is a morphological variety of *V. convallaria*.
V. simplex Nenninger, 1948 closely resembles *V. longifilum*.
V. singularis Kahl, 1933 = *V. verrucosa* Dons, 1915.
V. smaragdina Stokes, 1885 is distinguished by its green colouration, a feature which was rejected by Noland & Finley (1931) for separating species. It now becomes a *nomen dubium*.
V. solitaria Stiller, 1935 closely resembles *V. subprocumbens* Ghosh, 1922.
V. spectrabilis Kent, 1881 is a distinct species which Kahl (1935) renamed *V. kenti* in order to solve the problem of homonymy with Bory's (1824) *V. spectrabilis*.
V. sphaerica d'Udekem, 1864 = *V. globularia*.
V. striata Dujardin, 1841 (p. 41).
V. striata var. *octava* (Stokes, 1885) Noland & Finley, 1931 was the name which Noland & Finley (1931) applied to Stokes' (1885) freshwater variety of *V. striata*. It is no longer recognised as a separate taxon.
V. striata var. *octava* f. *utriculus* Szczepanowski, 1978 = *V. infusionum*.
V. subconica Stiller, 1946 appears to be identical to *Vorticella* (*Pseudovorticella*) *punctata*.
V. subcylindrica Ghosh, 1922 appears to be synonymous with *V. elongata* Fromentel, 1874.
V. submicrostoma Ghosh, 1922 = *V. microstoma*.
V. suboctava Sommer, 1951 is an epizooic variety of *V. striata*.
V. subprocumbens Ghosh, 1922 (p. 42).
V. subsinuata Ghosh, 1922 (p. 43).
V. subsphaerica Dons (1915) 1918 is probably a morphological variety of *V. communis*.
V. szczepanowskii (Szczepanowski, 1978) nom. nov. for *V. plicata* Szczepanowski, 1978 (p. 43).

V. telescopica Kent, 1881 (p. 43).
V. telescopica Kahl, 1935 was renamed *V. telescopoides* by Šramek-Hušek (1948*b*) in order to prevent homonymy with the previous species.
V. telescopica var. *marina* is a marine variety of Kent's (1881) *V. telescopica*.
V. telescopiformis (Gourret & Roeser, 1886) Kahl, 1935 = *V. telescopica* Kent, 1881.
V. telescopoides (Kahl, 1935) Šramek-Hušek, 1948 (p. 44).
V. teninucleata Dons, 1922 is a poorly characterised marine species which was described from contracted specimens. It therefore becomes a *nomen dubium*.
V. turgicula Wang Jiaji, 1977 (p. 44).

V. undulata (Dons, 1918) Kahl, 1935 has a short, straight spasmoneme and was originally called *Vorticellopsis undulata*. It was so poorly described that it is now regarded as a *nomen dubium*.
V. urceolus Biernacka, 1963 is probably a morphological variety of Stiller's (1953*b*) *V. carinogammari* (= *Haplocaulis carinogammari*).
V. urnula Nenninger 1948 closely resembles *V. globosa*.
V. utriculus Stokes, 1885 is probably a variant of .*V infusionum*.

V. variabilis Stiller, 1939 is probably a marine variety of *V. bidulphae*.
V. venusta Nenninger, 1948 (p. 44).
V. vernalis Stokes, 1887 (p. 45).
V. verrucosa Dons, 1915 (p. 45).
V. vestita Stokes, 1883 (p. 45).
V. voeltzkowi Sondheim, 1929 (p. 47).
V. zooanthelligera Stiller, 1968 has rows of regularly arranged pellicular tubercles and should therefore be transferred to the genus *Pseudovorticella*.

British Museum (Natural History)

The littorinid molluscs of mangrove forests in the Indo-Pacific region

D. G. Reid

Periwinkles (family Littorinidae) are amongst the most intensively studied of marine gastropods, because of their worldwide distribution and abundance in the intertidal environment. This monograph is a comprehensive account of the taxonomy, biology and biogeography of the *'Littorina scabra'* species complex, a hitherto poorly-known group of littorinids ubiquitous in mangrove habitats throughout the Indo-Pacific region. Twenty species are recognized, where most previous authors have distinguished only three. Detailed accounts of the anatomy of each species are given, with particular attention to the reproductive system, by which the species can be reliably distinguished. A key to shells is provided, and 100 figures and plates illustrate the range of shell variation, anatomical characters and geographical distribution of each species.

Drawing on comparisons with ten littorinid genera, evolutionary trends in the morphology of male and female reproductive tracts, sperm nurse cells, egg capsules, reproductive modes and radulae are discussed. These features are assessed as taxonomic characters, and the large literature on the morphology of the family is reviewed. Cladistic analysis of anatomical characters supports a reclassification of the Littorinidae, including placement of the *'scabra'* group in the genus *Littoraria*.

In addition to molluscan systematists, this monograph should be of interest to marine biogeographers and ecologists working in the mangrove environment. In recent years much ecological and genetical research has been stimulated by the discovery of sibling species of *Littorina* in Europe. The *Littoraria* species have a similar potential in the Indo-Pacific, where up to ten species may occur sympatrically. Several of the species are polymorphic for shell colour and have already been used as material for the study of mechanisms of natural selection.
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A revision of the Suctoria (Ciliophora, Kinetofragminophora) 4. *Podophrya* and its morphological relatives

Colin R. Curds
Zoology Department, British Museum (Natural History), Cromwell Road, London SW7 5BD

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Introduction

The species of the two well-known genera *Podophrya* Ehrenberg, 1833 and *Sphaerophrya* Claparède and Lachmann, 1859 and the two lesser known *Parapodophrya* Kahl, 1931 and *Mucophrya* Gajewskaja, 1933 are the subjects for consideration in this the fourth part of the series. It will immediately be noticed that the genus *Sphaerophrya* has here been treated as a synonym of *Podophrya*. The two genera were originally distinguished by the presence of a stalk in *Podophrya* and the absence of one in *Sphaerophrya*. However it has long been known that the stalk is often lost by several species of *Podophrya* and apparently some *Sphaerophrya* species occasionally develop one. The presence of a cyst with a stalk has also been used as a distinguishing character but it should be appreciated that this is based on few observations and a similar stage may yet be found in *Sphaerophrya*. Another possible method of distinguishing the two genera investigated by the present author was based on the observation that the ciliary rows in *Podophrya* species are arranged transversely while those in many traditional *Sphaerophrya* species are arranged longitudinally. However examination of the description of bud formation in the type species *Podophrya fixa* Ehrenberg, 1833 by Penard (1920) clearly shows that while the kineties are initially transverse they become longitudinally orientated as the bud elongates. It is clear therefore that there is no stable character by which to distinguish the two genera and under such circumstances they must be synonymised, indeed Corliss (1979) indicated that such a step might be necessary in his taxonomic review of the ciliates.

Genus *PODOPHRYA* Ehrenberg, 1833

Sphaerophrya Claparède and Lachmann, 1859
Kystopus Jankowski, 1967

The morphology of *Podophrya* is simple in comparison to many other suctoria and several features indicate that they could be regarded as primitive. Most are simple spheres with an even distribution of capitate tentacles radiating out from the body. Some are without a stalk and float freely in the water while others are attached by means of a stalk to vegetation and inanimate objects, only rarely are they found attached to aquatic arthropods. Several species have become endo- or ectoparasites of ciliated protozoa and in some cases the species may only be distinguished by its association with a particular host. However, it should be noted that the degree

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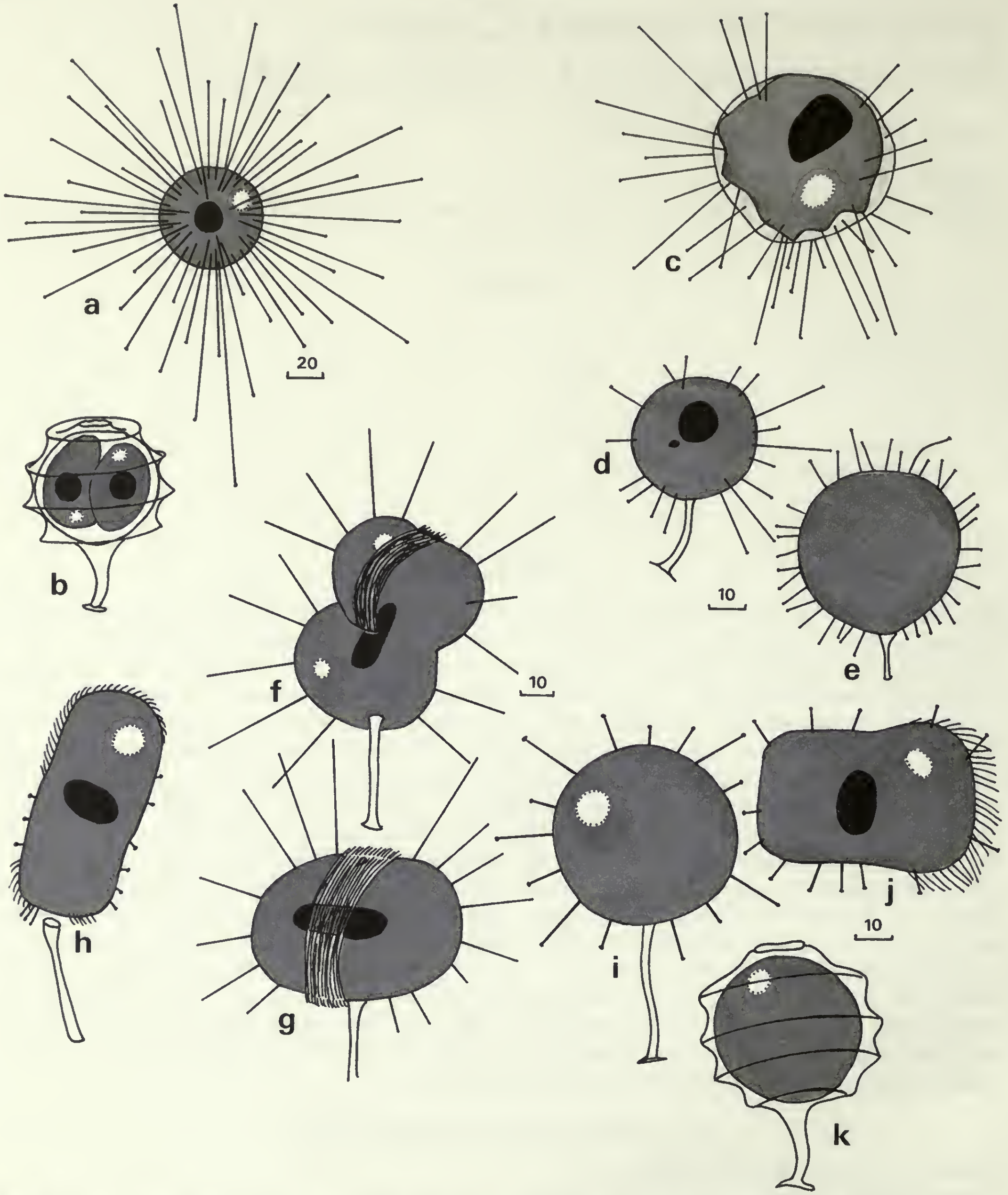

Fig. 1. *Podophrya fixa:* (a,b) adult and cyst after Collin, 1912; (c) after Fukui & Morishita, 1962 (called *P. variabile*); (d) after Ghosh, 1929 (called *P. bengalensis*); (e) after Sand, 1899 (called *P. brevipoda*); (f,g,h) budding and transformation of adult into motile form after Penard, 1920; (i,j,k) adult, embryo and cyst after Collin, 1912.

of specificity of these parasites has not been determined and some may be further synonymised as more information becomes available.

The relatively primitive nature of *Podophrya* is shown by its method of reproduction which, in contrast to the other genera so far considered (Curds, 1985*a, b, c*), is by a type of external budding known as 'pseudo-scissiparité' (Batisse, 1975). In this type of budding the mother cell enlarges and divides across the cell as is the normal method of division in ciliates but here a field of kinetosomes migrates from the mother to become the ciliary bases of the motile bud (see Fig. 1f). The cilia initially develop as transverse rows but in some cases these may later develop into longitudinal rows because of elongation by the bud in that axis. Some species have been reported to have the ability for the whole cell to transform itself (Fig. 1g, h) into a motile bud-like form which is rather reminiscent of telotroch formation in the peritrichs and presumably plays a similar role in enabling the organism to move away from one attachment site to another if necessary. Cyst formation is well documented in several species of *Podophrya*. Cysts are generally stalked and heavily ribbed and the numbers of ribs have been used as criteria for species identification. Multiple fission of the suctorian within the cyst has been reported in *Podophrya*.

Diagnosis of *Podophrya*

Typically freshwater, rarely marine, suctorians whose outline shape varies from spherical to ovoid. Lorica absent, some species borne upon a stalk but this may often be absent. Some species free-living, others are parasitic in or on other ciliates. Free-living species usually attached to aquatic vegetation or inanimate objects and only rarely to invertebrates. Tentacles reduced in the parasitic species but are capitate, long and numerous in the free-living ones. Tentacles distributed all over body, not in fascicles. Actinophores absent. Cysts sometimes stalked and often heavily ribbed. Reproduction by external buds (division into parts), buds ciliated with 3–12 rows of cilia that initially develop transversely. In some cases the ciliary rows become transformed into longitudinal rows as the bud elongates. Buds usually with rudimentary tentacles. Whole cell may convert into a motile bud-like state.

Key to the species of *Podophrya*

1	Free-living	2
	Parasitic	25
2	With stalk	3
	Without stalk	14
3	Ectocommensal on marine crustacea, stalk very short	***P. niphargi***
	Not on crustacea, stalk at least half body length	4
4	Many tentacles present	5
	Only 2 tentacles present	***P. flexilis***
5	Tentacles of same length	7
	Tentacles of two different lengths	6
6	Freshwater, long mobile tentacles	***P. globulifera***
	Brackish, long immobile tentacles	***P. halophila***
7	Stalk striated transversely	***P. fallax***
	Stalk not striated	8
8	Diameter of zooid less than 15 µm	9
	Diameter of zooid greater than 20 µm	10
9	Several contractile vacuoles present	***P. spenceri***
	Single contractile vacuole present	***P. gracilis***
10	Stalk widens markedly at junction with zooid	***P. macrostyla***
	Stalk more or less parallel with zooid	11
11	Thick external layer to zooid	***P. maupasi***
	No thick external layer to zooid	12
12	Body spherical	13
	Body spherical but has posterior projection at junction with stalk	***P. sandi***
13	Stalked cyst with 4 ribs	***P. fixa***
	Stalked cyst with many (about 12) ribs	***P. libera***
14	Body hemispherical, attached by body side	***P. simplex***
	Body ovoid or spherical, not attached by body side	15
15	Without contractile vacuole, macronucleus elongate	***P. massiliensis***
	With contractile vacuole, macronucleus spherical to ovoid	16
16	Single contractile vacuole	21
	Two or more contractile vacuoles	17

17	Several contractile vacuoles	18
	Two contractile vacuoles	19
18	Spherical body, floats with aid of non-pulsating gaseous vacuole	***P. hydrostatica***
	Oval body, without gaseous vacuole	***P. ovata***
19	Tentacles few (<10)	***P. natans***
	Tentacles many (>30)	20
20	Tentacles grouped in bunches	***P. melosirae***
	Tentacles randomly distributed	***P. magna***
21	Capable of movement by use of tentacles or body	23
	Static, cannot move by use of tentacles	22
22	Tentacles restricted to one small area of body	***P. parva***
	Tentacles distributed all over body surface	24
23	Body shape always spherical	***P. libera***
	Body shape changeable, often irregular	***P. amoeboides***
24	Tentacles tend to be long, forms stalked cyst	***P. libera***
	Tentacles tend to be short, without stalked cyst	***P. sol***
25	Suctoria attached to surface of ciliate host	26
	Suctoria lie beneath surface of ciliate host	30
26	Body spherical, tentacles without wide bases	27
	Body irregular, tentacles with wide bases	***P. atypica***
27	Attached to *Nassula* in clusters	***P. parasitica***
	Different host	28
28	Attached to *Stokesia* in clusters	***P. stokesii***
	Different host	29
29	Attached to hypotrichs (*Oxytricha, Stylonychia* and *Paruroleptus*)	***P. pusilla***
	Attached to *Vorticella* in clusters	***P. epizooica***
30	Suctoria lie in open surface pockets in cytoplasm of ciliate host	31
	Suctoria lie deep within cytoplasm of ciliate host	32
31	Lies in cytoplasmic pockets of *Nassula*	***P. iftodi***
	Lies in cytoplasmic pockets of *Stylonychia lemnae*	***P. grelli***
32	Contained within host *Stentor*	37
	Contained within other hosts	33
33	Contained within host *Paramecium*	***P. parameciorum***
	Contained within other hosts	34
34	Contained within hypotrichs	35
	Contained within host *Bursaria*	***P. insolita***
35	Bud has cilia in transverse rings	***P. pusilla***
	Bud has cilia arranged longitudinally	36
36	Lies within oral funnel of *Euplotes*	***P. canelli***
	Lies within body of *Urostyla* or *Stylonychia*	***P. urostylae***
37	Bud with 2 contractile vacuoles and capitate tentacles	***P. stentoris***
	Bud with 1 contractile vacuole and non-capitate tentacles	***P. doliolum***

Species descriptions of *Podophrya*

Podophrya fixa (Muller, 1786) Ehrenberg, 1833

Trichoda fixa Muller, 1786
Peritricha cometa Bory, 1825
Actinophrys pedicellata Dujardin, 1841
Orcula trochus Weisse, 1847 (the cyst)
Actinophrys difformis Perty, 1852
Actinophrys sol Stein, 1854 *pro parte*
Podophrya brevipoda Sand, 1899
Podophrya bengalensis Ghosh, 1929
Podophrya variabile Fukui and Morishita, 1962

DESCRIPTION (Fig. 1). This the type species is a small to medium (50–75 µm diameter), freshwater or marine, aloricate suctorian that is spheroidal in shape. Typically free-living but there is one report (Penard, 1920) of it as an endoparasite of the hypotrichous ciliate *Stylonychia mytilus* although perhaps it could have been *P. grelli.* Often, but not always, borne upon a stalk that is variable in length but usually about the same length as the body diameter. Tentacles capitate, variable in length, radiating out from all over surface of body. Free-living forms attached to vegetation and inanimate objects. Macronucleus ovoid and centrally located. Single contractile vacuole. Adult has ability to totally transform into a ciliated bud-like form (Fig. 1f) enabling it to swim away from its stalked attachment to a more favourable site.

Reproduction by pseudo-scissiparity producing a bud that is approximately the same size as the mother cell with about 12 longitudinal rows of cilia and several rudimentary tentacles. Well developed stalked cyst produced with 4 prominent transverse ribs. Fission can occur within cyst to produce up to 4 daughter cells (Fig. 1b).

Podophrya amoeboides (Sand, 1899) n. comb.

Trichophrya amoeboides Sand, 1899
Trichophrya variabilis Sand, 1899

Description (Fig. 2). Small (15–40 µm long), freshwater or marine, aloricate suctorian that is oval, lozenge, pyriform or irregular with lobes. Body able to slowly change its shape. Free-living, without stalk, found amongst algae and hydroid colonies. Tentacles capitate, of variable length and radiating out from all over the body surface. Movement is achieved by means of tentacles and body changes. One tentacle is extended forward and attaches itself distally. It then contracts and pulls the entire organism forward. The action apparently deforms the body by elongating that part of the cytoplasm to which the contracting tentacle is attached, although Penard (1920) states that this species can also move by means of its body in a manner comparable to leucocytes. Central spherical macronucleus, single anterior or central contractile vacuole. Reproduction and budding not described but Penard (1920) saw a bud, which he suspected to derive from this

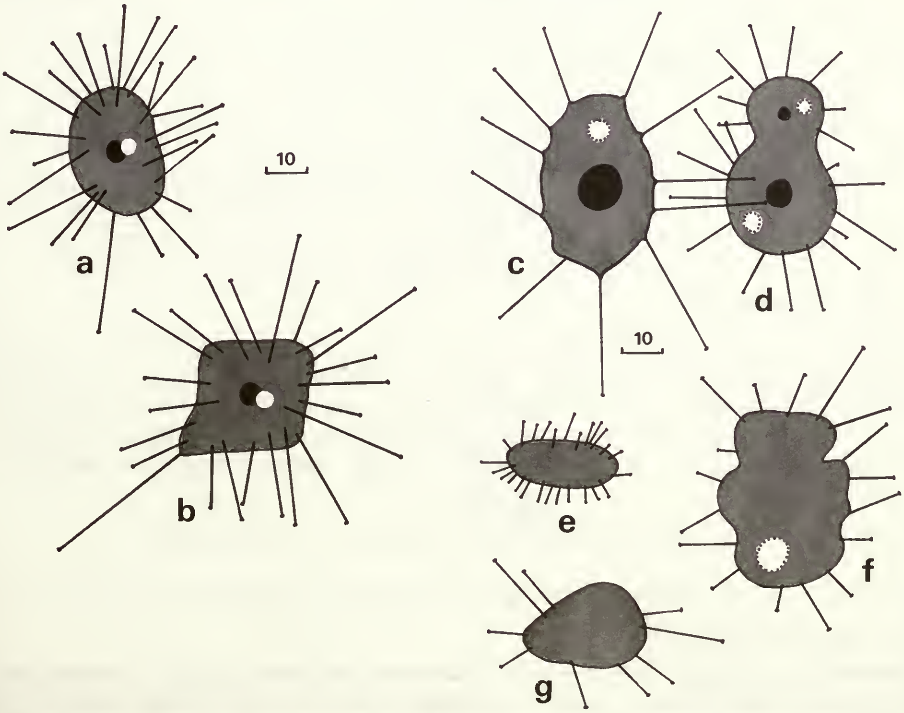

Fig. 2. *Podophrya amoeboides:* (a,b) after Sand, 1899 (called *Trichophrya amoeboides*); (c,d) after Penard, 1920 (called *Trichophrya variabilis*); (e,f,g) after Sand, 1899 (called *Trichophrya variabilis*).

species, that was an elongated ovoid covered in ciliary rows. Cyst formation also thought to occur (Penard, 1920).

Note. Since Penard (1920) discovered *T. variabilis* in salt water there seems to be no reason for distinguishing between it and *T. amoeboides*. The latter mentioned species takes precedence since it was described on an earlier page than *T. variabilis*.

Podophrya atypica (Gonnert, 1935) n. comb.

Parapodophrya atypica Gonnert, 1935

Description (Fig. 3). Small (10 µm diameter), freshwater, aloricate suctorian that is highly irregular in shape. Ectoparasitic on the ciliate *Colpoda*. Tentacles prominently capitate, length about three times body diameter, bases greatly expanded. One tentacle firmly embedded into cytoplasm of host cell. Ovoid macronucleus and single contractile vacuole centrally positioned. Mode of reproduction and bud morphology undescribed.

Note. Until the bud and budding are fully described the true taxonomic position for this species will be unknown. However it was thought more advisable to transfer it to *Podophrya* since all other species of *Parapodophrya* are free-living and the similarity in tentacles was not considered to be sufficient to retain it in the latter genus.

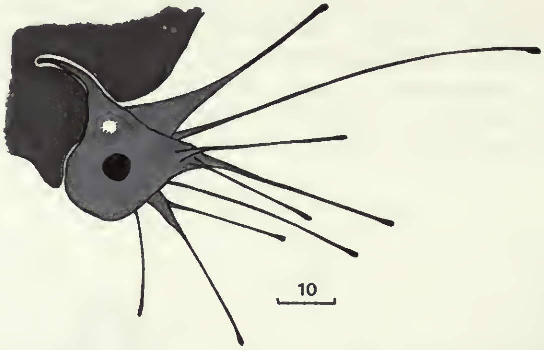

Fig. 3. *Podophrya atypica* after Gonnert, 1935 (called *Parapodophrya atypica*).

Podophrya canelli (Clement, 1967) n. comb.

Sphaerophrya canelli Clement, 1967

Description (Fig. 4). Small (10–25 µm diameter), freshwater, spherical, aloricate suctorian. Endoparasite of the hypotrichous ciliates *Euplotes eurystomus* and *E. patella*, usually located in the peristomial depression of the host cell. Stalk absent. Some short capitate tentacles present randomly distributed over body surface. Central spherical macronucleus, single contractile vacuole. Reproduction by pseudo-scissiparity. Bud ovoid with 4 or 5 parallel longitudinal rows of cilia. Cyst not formed.

Note. Originally described by Canella (1957) but not given a specific name.

Podophrya doliolum (Penard, 1920) n. comb.

Sphaerophrya doliolum Penard, 1920

Description (Fig. 5). Small (25–35 µm diameter), freshwater, spherical, aloricate suctorian. Parasitic in surface cytoplasmic pockets in the ciliate *Stentor niger*. Stalk absent. Few short tentacles in adult. Central ovoid macronucleus with well-displaced micronucleus. Single contractile vacuole. Reproduction by rapid pseudo-scissiparity forming groups of parasites in the

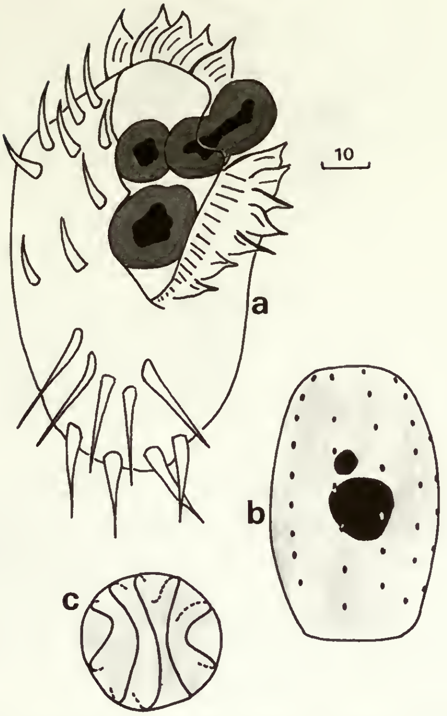

Fig. 4. *Podophrya canelli:* (a) adults inside host *Euplotes*; (b,c) embryos, lateral and apical aspects. All after Clement, 1967 (called *Sphaerophrya canelli*).

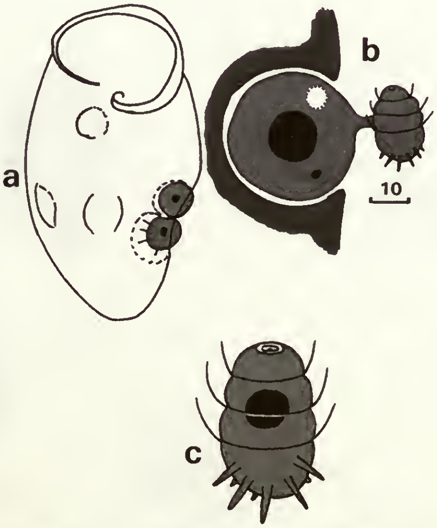

Fig. 5. *Podophrya doliolum:* (a) adults on host *Stentor;* (b,c) budding and embryo. All after Penard, 1920 (called *Sphaerophrya doliolum*).

host. Some buds develop into ovoid cilated embryos carrying 3 well-displaced transverse rings of cilia and rudimentary tentacles at the posterior end. An adhesive disc at the anterior pole.

NOTE. Penard distinguished this species from *Podophrya stentoris* on the basis of the ciliary rings and their distribution in *Podophrya doliolum*.

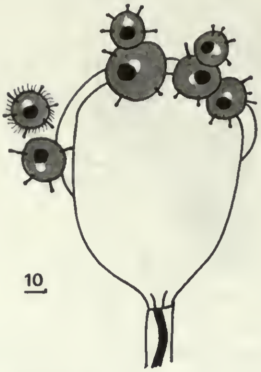

Fig. 6. *Podophrya epizoica* growing on *Vorticella campanula*, after Hammann, 1952.

Podophrya epizoica Hammann, 1952

Description (Fig. 6). Small (20–35 µm diameter), freshwater, spherical, aloricate suctorian. Ectoparasitic on the peritrichous ciliate *Vorticella campanula*, usually close to the peristomial lip. Stalk absent. Capitate tentacles randomly distributed over entire body surface but relatively few, about 6, in number. Attachment to the host is via a large embedded tentacle. Single contractile vacuole. Large central macronucleus. Reproduction by pseudo-scissiparity. Bud not described in detail but has cilia and rudimentary capitate tentacles.

Podophrya fallax Dingfelder, 1962

Description (Fig. 7). Medium (60 µm diameter), freshwater, spherical, aloricate suctorian. Free-living, borne upon stalk whose length is usually at least twice the body diameter. Stalk striated

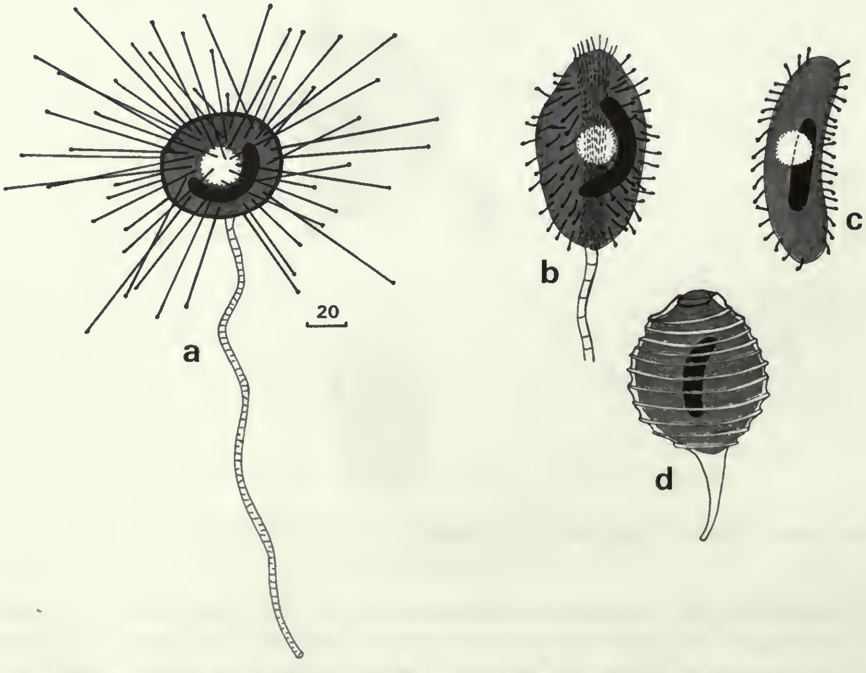

Fig. 7. *Podophrya fallax:* (a) adult; (b) transformation of adult into motile form; (c,d) embryo and cyst. All after Dingfelder, 1962.

transversely. Tentacles capitate, radiating out from all over surface of body. Attached to vegetation and inanimate objects in ponds. Macronucleus sausage-shaped, curving around the single central contractile vacuole. Adult has ability to totally transform itself into a ciliated bud-like form whose cilia are arranged in many longitudinal rows. Reproduction by pseudo-scissiparity producing a bud whose size approximates to that of the mother cell. Well developed stalked cyst produced with about 11 prominent ribs.

Podophrya flexilis Kellicott, 1887

Tokophrya flexilis (Kellicott, 1887) Butschli, 1889

Description (Fig. 8). Small (25–50 µm diameter), freshwater, ovoid, aloricate suctorian. Free-living, borne upon a stalk that is shorter than the body diameter. Attached to the stalks of the peritrichous ciliate *Epistylis digitalis* on the crustacean *Cyclops*. Capitate tentacles, few, 2–4, about six times as long as body diameter, extensible and flexible. Macronucleus ovoid, located in posterior body half. Contractile vacuole situated apically. Reproduction and bud not described.

Podophrya globulifera Kahl, 1931

Description (Fig. 9). Medium (50–70 µm diameter), freshwater, spherical, aloricate suctorian. Free-living, borne upon a stalk whose length is about twice the body diameter. Tentacles of two

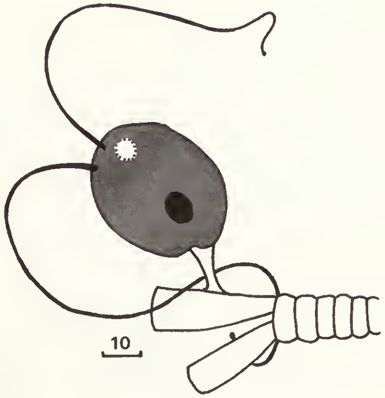

Fig. 8. *Podophrya flexilis* after Kellicott, 1887.

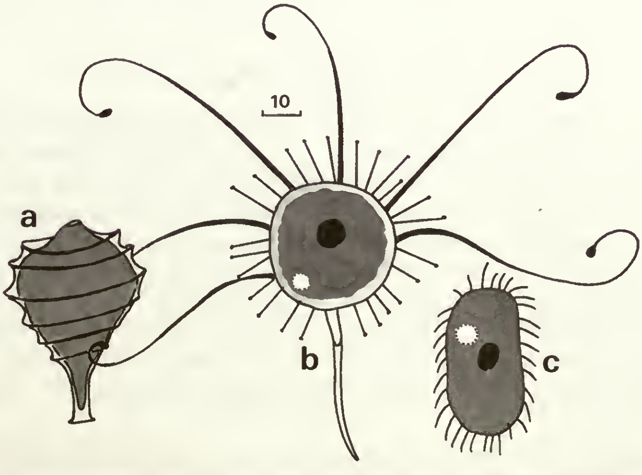

Fig. 9. *Podophrya globulifera:* (a,b,c) cyst, adult and embryo after Kahl, 1931.

types, many short capitate tentacles and fewer long, extensible capitate tentacles. Fascicles absent, tentacles radiate out from all over body surface. Attached to vegetation and inanimate objects. Spherical macronucleus centrally located, single contractile vacuole. Reproduction by pseudo-scissiparity producing buds whose ciliary rows are longitudinally orientated. Well developed stalked cyst bearing about six prominent transverse ribs.

Podophrya gracilis Calkins, 1902

DESCRIPTION (Fig. 10). Small (8 μm diameter), marine, spherical, aloricate suctorian. Free-living, borne upon a stalk whose length is about five times the body diameter. Body covered in short capitate tentacles. Attached to inanimate objects. Spherical macronucleus located in posterior half of body. One or two contractile vacuoles present. Reproduction and bud not described.

NOTE. Collin (1912) was of the opinion that this organism was a heliozoan but Kahl (1934) disagreed and the true status is still uncertain.

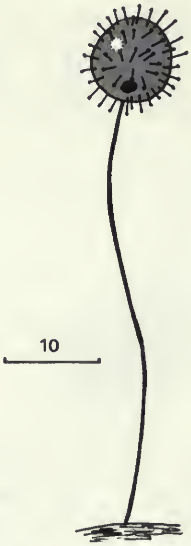

Fig. 10. *Podophrya gracilis* after Calkins, 1902.

Podophrya grelli Dieckmann, 1985

DESCRIPTION (Fig. 11). Small (25–50 μm diameter), freshwater, spherical, aloricate suctorian. Free-living or endoparasitic in the hypotrichous ciliate *Stylonychia lemnae* in which it lies just beneath the surface in cytoplasmic pockets that remain open to the external environment. Parasite is apparently host-specific. Few short capitate tentacles when inside host. Ciliated buds produced by unequal to equal exogenous budding. Conjugation of parasite occurs after degeneration of host. Stalked cysts with 5 ribs similar to those of *P. fixa* are produced outside host after conjugation. The final rib in *P. grelli* is directed posteriorly (Fig. 11) towards the stalk while that of *P. fixa* is directed posterio-laterally (Figs 1b, 1k). Multiple fission within cyst produces infective buds that are indistinguishable from buds of the asexual generation. Buds or swarmers small (15–20 μm long), oval with few rudimentary tentacles. There are 6–7 kineties and a bunch of posterior caudal cilia.

NOTE. This may be the suctorian parasite seen by Penard (1920) and thought to be *P. fixa* which is similar but not usually parasitic.

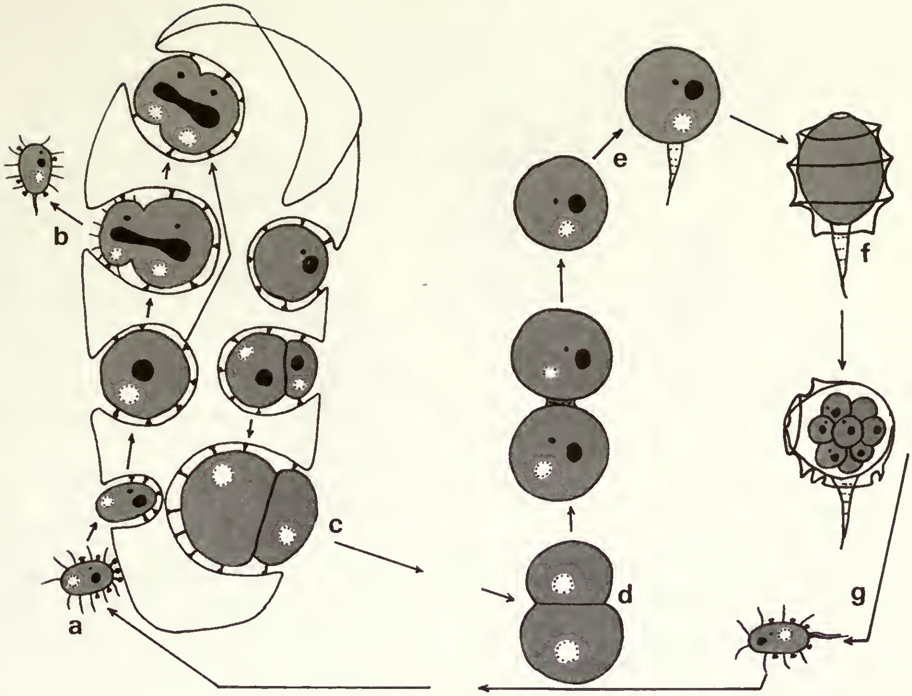

Fig. 11. *Podophrya grelli* after Dieckmann, 1985. Life cycle stages (a–c) inside host, (d–g) in culture fluid. (a) ciliated swarmer infects host; (b) budding produces more swarmers; (c) conjugation, conjugants released when host degenerates; (d) conjugants in culture medium; (e) exconjugant develops stalk; (f) stalked cyst; (g) swarmers produced after multiple division in cyst.

Podophrya halophila Kahl, 1934

Description (Fig. 12). Medium (50–90 µm diameter), marine, spherical, aloricate suctorian. Free-living, borne upon a stalk whose length approximates to that of the body diameter. Body covered in capitate tentacles of two lengths, many short tentacles and fewer tentacles that are about the same length as the body. Attached to inanimate objects. Spherical macronucleus, single contractile vacuole. Reproduction by pseudo-scissiparity producing buds whose ciliary kineties are longitudinally orientated. There are two contractile vacuoles in the bud.

Podophrya hydrostatica (Engelmann, 1878) n. comb.

Sphaerophrya hydrostatica Engelmann, 1878

Description (No figure). Medium (80–90 µm diameter), freshwater, spherical, aloricate suctorian. Free-living, without stalk, floating freely in water amongst *Lemna*. Body covered in many long capitate tentacles. Numerous small contractile vacuoles and a large, half body diameter, non-contractile gaseous vacuole to aid flotation of the organism. Reproduction and bud not described.

Note. Although apparently seen and described on several occasions, this species has not yet been figured.

Podophrya iftodi (Clement-Iftode, 1967) n. sp.

Sphaerophrya sp. Clement-Iftode, 1967

Description (Fig. 13). Small (10–30 µm diameter), freshwater, spherical, aloricate suctorian.

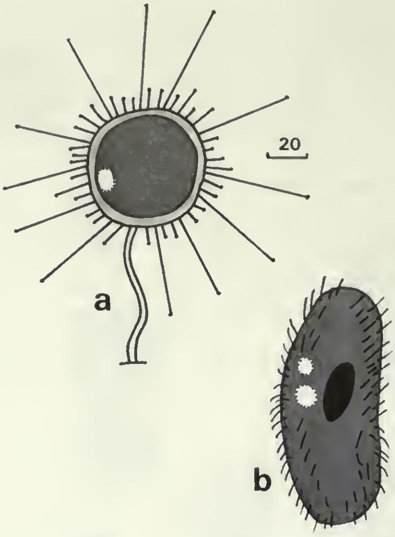

Fig. 12. *Podophrya halophila*: (a,b) adult and embryo after Kahl, 1934.

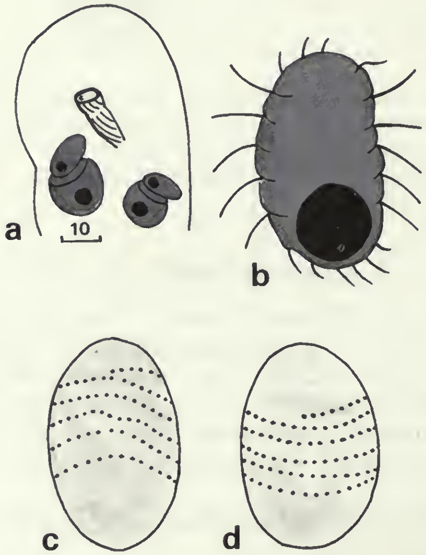

Fig. 13. *Podophrya iftodi:* (a) adults in host *Nassula elegans*; (b,c,d) embryos and ciliation. All after Clement-Iftode, 1967 (called *Sphaerophrya* sp.).

Parasitic in the ciliate host *Nassula elegans* where it inhabits pockets deep within the pellicle of the host. Stalk and cyst absent. Several short capitate tentacles distributed over body surface. Centrally located ovoid macronucleus. Reproduction by pseudo-scissiparity. Ovoid buds with 5 or 6 transversely orientated ciliary rings, and macronucleus in posterior position.

NOTE. Fauré-Fremiet (1945) described a suctorian parasite of *Nassula ornata* which he called *Podophrya parasitica*. This can easily be distinguished from *Podophrya iftodi* by several features. *P. parasitica* remains on the surface of the host and does not live in pockets. Furthermore its buds have longitudinally orientated ciliary lines.

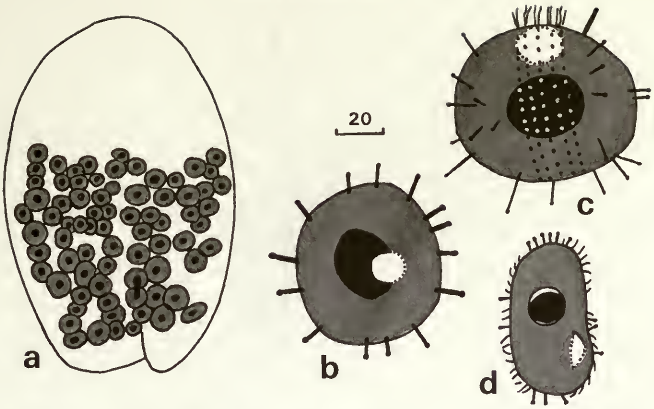

Fig. 14. *Podophrya insolita:* (a) adults in host *Bursaria;* (b,c,d) adult and embryos. All after Jankowski, 1973.

Podophrya insolita Jankowski, 1973

Description (Fig. 14). Medium (50–80 µm diameter), freshwater, spherical, aloricate suctorian. Endoparasite of the ciliate *Bursaria truncatella.* Stalk and cyst absent. Several short capitate tentacles randomly distributed over body surface. Centrally located macronucleus. Reproduction by pseudo-scissiparity producing daughters that possess tentacles but not cilia. Synchronous total transformation of daughter cells into motile forms called 'trophotomites' enables the infestation to be transmitted from host to host. Young trophotomites with above five transverse ciliary rings elongate into mature laterally flattened oval tomites with longitudinal kineties and some rudimentary tentacles.

Podophrya libera Perty, 1852

Podophrya fixa var. *algeriensis* Maupas, 1876

Description (Fig. 15). Small to medium (30–80 µm diameter), freshwater, spherical, aloricate suctorian. Free-living, sometimes borne upon a slender stalk whose length approximates to that of the body but often detached and floating freely in the water. Body covered with many capitate tentacles of three different lengths from 3 to 6 times the body length. Centrally located spherical macronucleus, single marginal contractile vacuole. Cyst spheroidal, stalked, carrying 8–16 prominent transverse rings. Reproduction by pseudo-scissiparitous budding producing an unciliated bud which then totally transforms into a ciliated motile form.

Podophrya macrostyla Stokes, 1885

Discophrya macrostyla Collin, 1912

Description (Fig. 16). Medium (50–55 µm diameter), freshwater, spherical, aloricate suctorian. Free-living, attached via a stalk to inanimate objects and aquatic vegetation. Stalk wide, 8 µm, gradually enlarging to 15 µm when it forms a cup-like structure to join the zooid. Covered in capitate tentacles. Subcentrally located oval macronucleus, single marginal contractile vacuole. Reproduction and bud not described.

Podophrya magna (Maupas, 1881) n. comb.

Sphaerophrya magna Maupas, 1881
Sphaerophrya pusilla Sand, 1901 *pro parte*

Description (Fig. 17). Small to medium (35–50 µm diameter), freshwater, spherical, aloricate suctorian. Free-living, stalk absent. Covered in capitate tentacles whose extended lengths approximate to that of the body. Eccentric spherical macronucleus, one or two contractile vacuoles. Reproduction by pseudo-scissiparity.

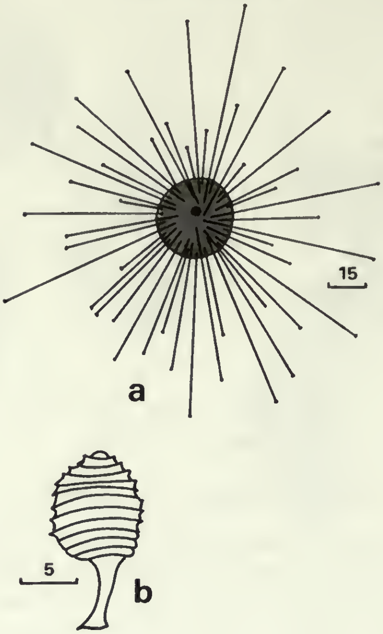

Fig. 15. *Podophrya libera:* (a) adult after Holm, 1925; (b) cyst after Spencer, 1917.

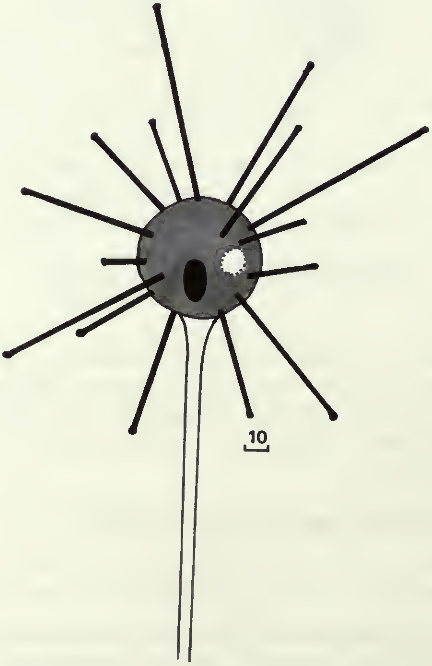

Fig. 16. *Podophrya macrostyla* after Stokes, 1885.

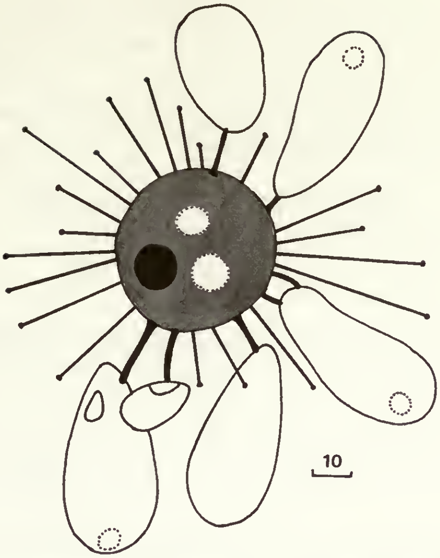

Fig. 17. *Podophrya magna* after Maupas, 1881 (called *Sphaerophrya magna*).

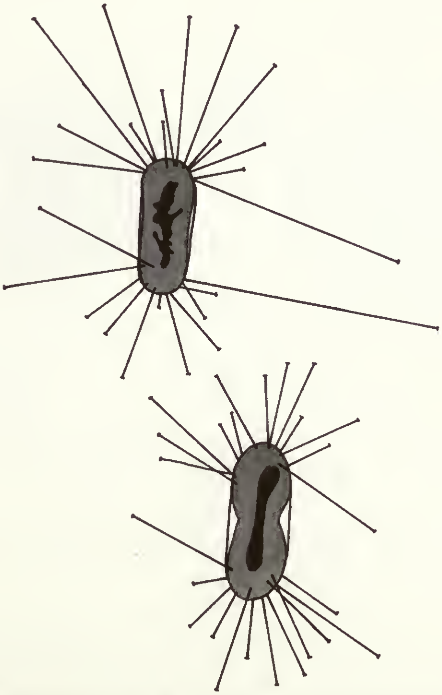

Fig. 18. *Podophrya massiliensis* after Gourret and Roeser, 1886 (called *Sphaerophrya massiliensis*). No scale given.

Podophrya massiliensis (Gourret and Roeser, 1886) n. comb.

Sphaerophrya massiliensis Gourret and Roeser, 1886
Trichophrya massiliensis Kahl, 1934

DESCRIPTION (Fig. 18). Marine, elongated ovoid to cylindrical, aloricate suctorian. Free-living, stalk absent. Capitate tentacles restricted to either end of body. Central region of body slightly narrower than ends so that the cell membrane visible in this region. Macronucleus, elongate and sometimes irregular. Contractile vacuole absent. Reproduction by pseudo-scissiparity. Buds not described.

NOTE. The transfer of this species into the genus *Trichophrya* by Kahl (1934) cannot be supported since the latter mentioned genus buds endogenously.

Podophrya maupasi Butschli, 1889

Podophrya fixa forma *typica* Maupas, 1876
Podophrya sp. Maupas, 1881
Podophrya or *Sphaerophrya* sp. Florentin, 1899

DESCRIPTION (Fig. 19). Small to medium (16–60 µm diameter), freshwater to brackish, spherical, aloricate suctorian. Free-living, borne upon a stalk that is approximately the same length as the body. Attached to aquatic vegetation and inanimate objects. Covered in 15–20 tentacles that are distributed over the entire body surface. Tentacles slightly trumpet-shaped at their ends. Spherical macronucleus centrally positioned, single marginal contractile vacuole. Cyst spherical, without ribs. Reproduction by pseudo-scissiparity, buds not described.

NOTE. Freshwater form larger (40–60 µm) than brackish-water form (16–22 µm).

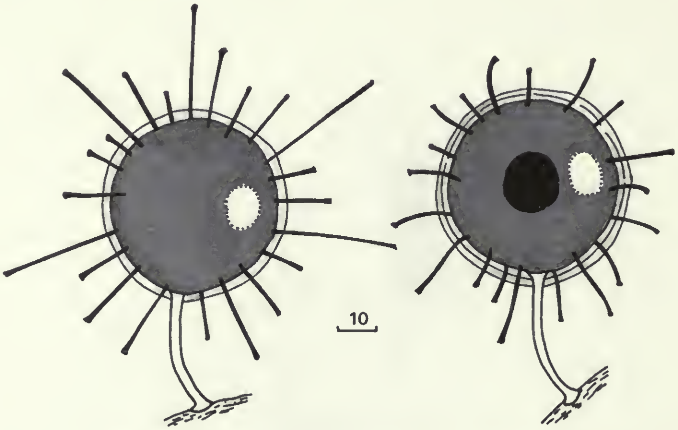

Fig. 19. *Podophrya maupasi* after Collin, 1912.

Podophrya melosirae (Gajewskaja, 1933) n. comb.

Sphaerophrya melosirae Gajewskaja, 1933

DESCRIPTION (Fig. 20). Medium (90 µm wide), freshwater, ovoid, aloricate suctorian. Free-living, stalk absent. Attached to aquatic vegetation by the body. Covered in long capitate tentacles that are grouped together in bundles. Spherical centrally positioned macronucleus. Two contractile vacuoles. Reported from Lake Baikal. Reproduction by pseudo-scissiparity.

Podophrya natans (Penard, 1920) n. comb.

Sphaerophrya natans Penard, 1920

DESCRIPTION (Fig. 21). Small (25 µm diameter), freshwater, irregularly ovoid, aloricate suctorian. Free-living, stalk absent. Attached to aquatic vegetation and inanimate objects. Few, 5 or 6, long capitate tentacles project from various parts of the cell surface. Spherical central macronucleus, two contractile vacuoles. Reproduction and buds not described.

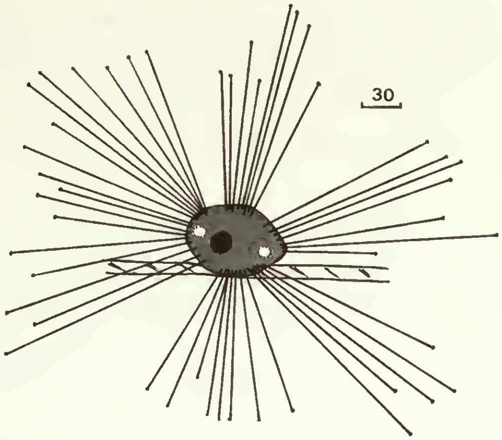

Fig. 20. *Podophrya melosirae* after Gajewskaja, 1933 (called *Sphaerophrya melosirae*).

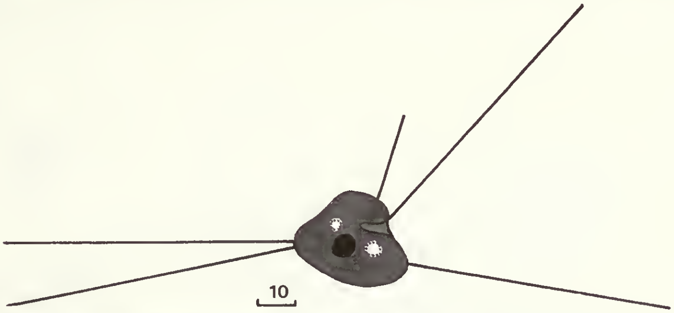

Fig. 21. *Podophrya natans* after Penard, 1920 (called *Sphaerophrya natans*).

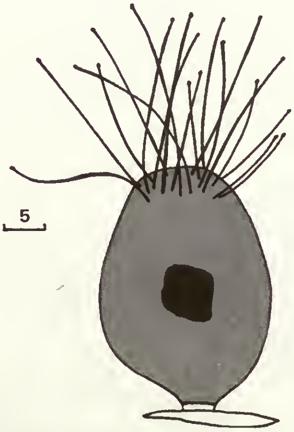

Fig. 22. *Podophrya niphargi* after Strouhal, 1939.

Podophrya niphargi Strouhal, 1939

DESCRIPTION (Fig. 22). Small (24–40 µm long), marine, ovoid, aloricate suctorian. Ectocommensal on the amphipod *Niphargus*. Capitate tentacles restricted to anterior surface only. Stalk very short, only a few microns long, but with a large basal plate. Central ovoid macronucleus. Reproduction thought to be by exogenous budding although original author was not certain. Buds not described.

NOTE. The position of this species in the genus *Podophrya* should be regarded with caution. There are several features which suggest that this is not the correct genus but the indication that it reproduces by external buds makes it difficult to find a more suitable taxonomic position.

Podophrya ovata (Weisse, 1847) n. comb.

Actinophrys ovata Weisse, 1847
Sphaerophrya ovata Lachmann, 1859

DESCRIPTION (Fig. 23). Freshwater, ovoid, aloricate suctorian. Free-living, stalk absent. Covered in capitate tentacles attached to aquatic vegetation. Two groups of three contractile vacuoles arranged at either end of the cell. Reproduction and buds not described.

Podophrya parameciorum (Maupas, 1881) Jankowski, 1963

Sphaerophrya pusilla Mechnikov, 1864
Sphaerophrya parameciorum Maupas, 1881
Podophrya parameciorum incursella Jankowski, 1963

DESCRIPTION (Fig. 24). Small (32 μm diameter), freshwater, spherical aloricate suctorian. Ectoparasite of several species of *Paramecium*. Few short capitate tentacles distibuted randomly

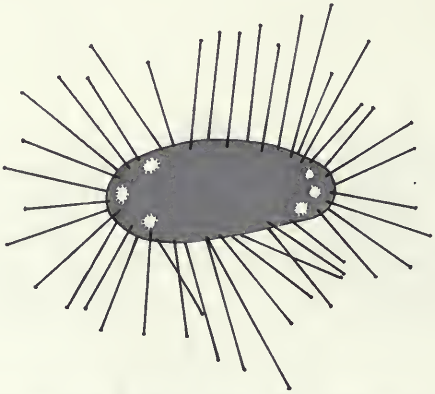

Fig. 23. *Podophrya ovata* after Weisse, 1847 (called *Actinophrys ovata*). No scale given.

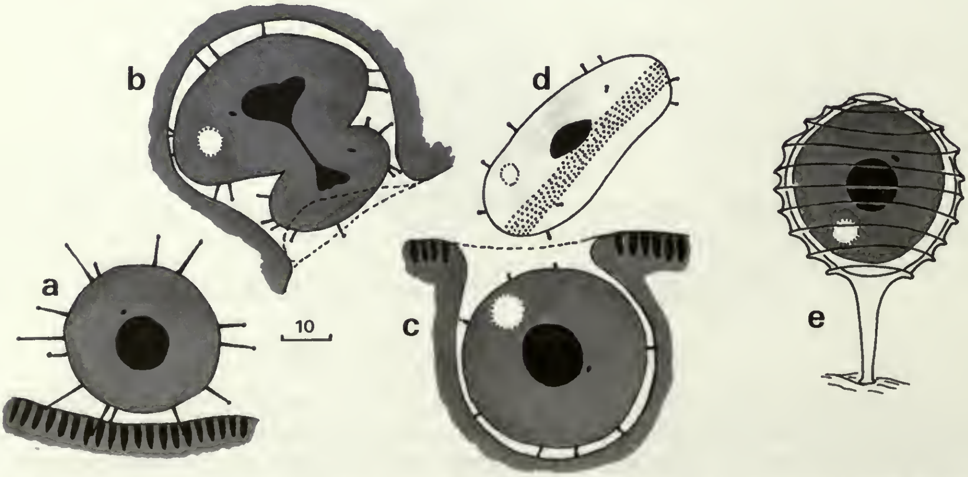

Fig. 24. *Podophrya parameciorum*: (a) adult on outside of host *Paramecium*; (b,c) parasites embedded in pockets in host cytoplasm; (d,e) embryo and cyst. All after Jankowski, 1963.

over surface area. Lives in open pockets in the cytoplasm of the host. Central spherical macronucleus, single marginal contractile vacuole. Reproduction by pseudo-scissiparity. Ciliated buds produced which have six longitudinal kineties. Adult can also exist outside of host and is capable of producing a stalked cyst with about ten prominent transverse ridges.

Note. Mechnikov (1864) was the first to describe a suctorian parasite of *Paramecium* which he mistook for *Sphaerophrya pusilla*.

Podophrya parasitica Fauré-Fremiet, 1945

Description (Fig. 25). Small (25–50 µm diameter), freshwater, spherical aloricate suctorian. Ectoparasite of *Nassula ornata*. Attached to exterior of host by capitate tentacles that radiate out from the entire surface area of the body. Always remains on the surface of the host, never beneath in pockets usually located at the posterior end of the host. Stalk absent. Large central spherical macronucleus, single marginal contractile vacuole. Reproduction by pseudo-scissiparity producing buds with about 7 rows of longitudinally orientated cilia and a few posterior rudimentary tentacles. Adult can exist attached to inanimate objects and encyst producing a stalked cyst with five prominent ridges.

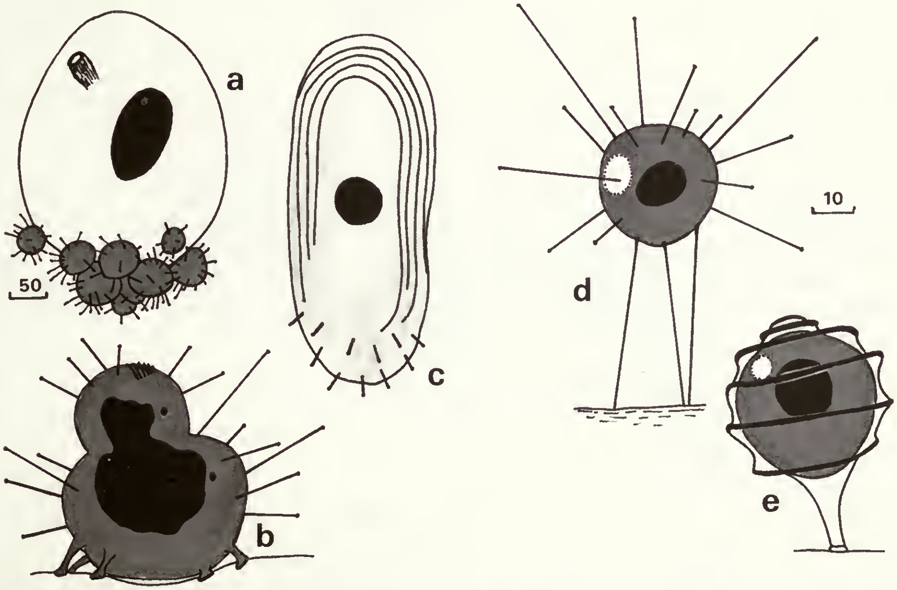

Fig. 25. *Podophrya parasitica:* (a) adults on host *Nassula ornata;* (b) budding; (c) ciliation of embryo; (d,e) adult and cyst. All after Fauré-Fremiet, 1945 except (c) which is after Guilcher, 1951.

Podophrya parva Greef, 1888

Description (No figure). Medium (90 µm diameter), freshwater, spherical aloricate suctorian. Free-living, attached by tentacles to moss. Tentacles long, capitate and restricted to a single zone on the body surface. Spherical macronucleus located centrally, single marginal contractile vacuole. Reproduction and bud not described and species remains unillustrated.

Podophrya pusilla (Claparède and Lachmann, 1859) n. comb.

Sphaerophrya pusilla Claparède and Lachmann, 1859
Sphaerophrya parurolepti Foissner, 1980

Description (Fig. 26). Small (12–50 µm diameter), freshwater to brackish, spherical, aloricate suctorian. Parasitic on hypotrichous ciliates such as *Oxytricha, Stylonychia mytilus* and

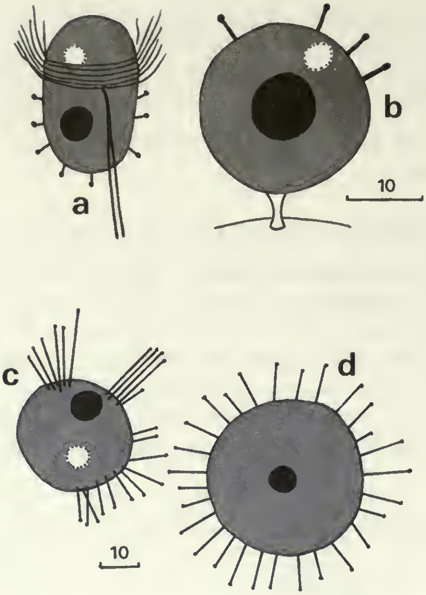

Fig. 26. *Podophrya pusilla:* (a,b) embryo and adult after Penard, 1920 (called *Sphaerophrya pusilla*); (c,d) adults after Gourret and Roeser, 1886 (called *Sphaerophrya pusilla*).

Paruroleptus caudatus. Reported to live on the outside of *Oxytricha* and *Paruroleptus* but the inside of *Stylonychia*. Capitate tentacles variable in number distributed all over surface of body but in some cases distribution may be rather patchy. Central spherical macronucleus, one or two contractile vacuoles. Reproduction by pseudo-scissiparity. Buds ciliated by about six closely packed transverse rows of cilia with 2 or 3 extra-long trailing cilia. Several rudimentary tentacles located in posterior half of bud.

Podophrya sandi Collin, 1911

Podophrya sp. Maupas, 1881
Podophrya sp. Simmons, 1889
Trichophrya gelatinosa Schewiakoff, 1893
Acineta gelatinosa Sand, 1896 *non Acineta gelatinosa* Buck, 1884

Description (Fig. 27). Small to medium (30–85 µm diameter), freshwater, spherical to ovoid, aloricate suctorian. Free-living, often, but not always, borne upon a narrow stalk that is approximately the same length as the body. Capitate tentacles emerge from all over body surface. Spherical macronucleus centrally located, single eccentric contractile vacuole. Reproduction by pseudo-scissiparity. Buds ovoid, bearing 8–10 longitudinal rows of cilia. Cyst spherical with 5 prominent ribs, without stalk.

Podophrya simplex (Zacharias, 1893) n. comb.

Acineta simplex Zacharias, 1893
Trichophrya simplex Sand, 1901

Description (No figure). Small (12 µm diameter), freshwater, hemispherical, aloricate suctorian. Free-living, attached by body to floating chains of *Fragilaria crotonensis*, stalk absent. Tentacles few, only 1 or 2, but measure five times the body diameter. Spherical central macronucleus, single contractile vacuole. Reproduction by pseudo-scissiparity. Buds not described.

Note. This species has been transferred to *Podophrya* because of its mode of budding. The two genera in the list of synonyms reproduce endogenously.

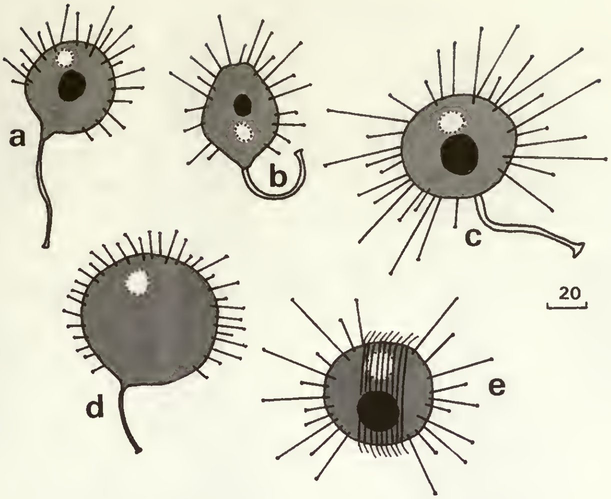

Fig. 27. *Podophrya sandi:* (a–e) various stages in life cycle after Collin, 1912.

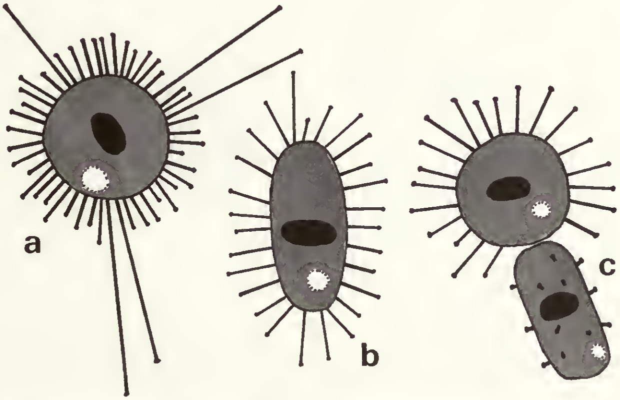

Fig. 28. *Podophrya sol* after Mechnikov, 1864 (called *Sphaerophrya sol*). No scale given.

Podophrya sol (Mechnikov, 1864) n. comb.

Sphaerophrya sol Mechnikov, 1864

DESCRIPTION (Fig. 28). Freshwater, spherical aloricate suctorian. Free-living, stalk absent. Many capitate tentacles, approximately half the body length, distributed all over body surface. Additionally there are few long capitate tentacles. Centrally positioned spherical macronucleus and up to three micronuclei. Single marginal contractile vacuole. Reproduction by pseudoscissiparity resulting in an ovoid bud with rudimentary capitate tentacles. Bud ciliation not described.

NOTE. Although Mechnikov (1864) originally described this species as a free-living suctorian later authorities including Kent (1882) and Collin (1912) misinterpreted his paper. Jankowski (1963) pointed out that Mechnikov (1864) described two suctorians, firstly *Sphaerophrya pusilla* (see *Podophrya parameciorum*) that was parasitic on *Paramecium* and secondly *Sphaerophrya sol* a free-living form.

Podophrya spenceri n. sp.

Tokophrya species 1 Spencer, 1917
Tokophrya species 2 Spencer, 1917

Description (Fig. 29). Small (10 µm long), freshwater, ovoid, aloricate suctorian. Free-living, borne upon stalk that may be branched to form a colony. Stalks two or three times length of body. Tentacles restricted to anterior body surface, few, 4–12, and capitate. Several contractile vacuoles. Reproduction and buds not described.

Note. This is a most doubtful species, as there are no other records of a branched stalk in the suctoria and it could be suspected that the organisms seen were perhaps not suctorians but peritrichous ciliates.

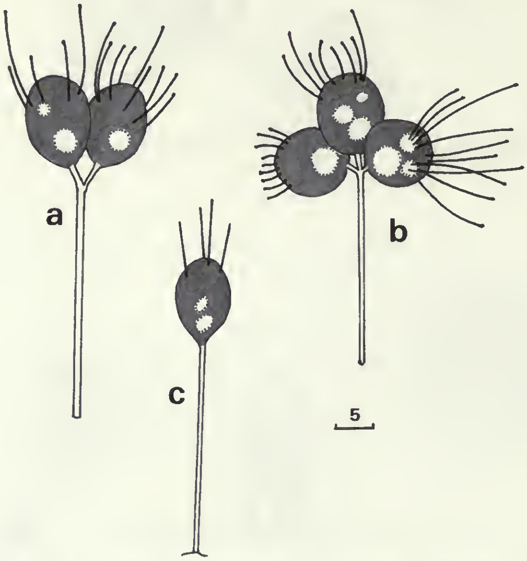

Fig. 29. *Podophrya spenceri:* (a,b) colonial forms (called *Tokophrya* sp. 1); (c) solitary form (called *Tokophrya* sp. 2). All after Spencer, 1917.

Podophrya stentoris (Maupas, 1881) n. comb.

Sphaerophrya stentoris Maupas, 1881
Sphaerophrya stentorea Sand, 1901

Description (Fig. 30). Small (35–45 µm diameter), freshwater, spherical, aloricate suctorian. Parasitic in *Stentor roeseli* and *S. coeruleus*. Adult with few short tentacles. Centrally located spherical macronucleus, single eccentric contractile vacuole. Reproduction by pseudo-scissiparity. Ovoid bud with anterior transverse ciliary rows, several posterior tentacles contractile vacuoles and is prominently waisted by the presence or two transverse grooves.

Podophrya stokesii (Mamaeva, 1979) n. comb.

Sphaerophrya stokesii Mamaeva, 1979

Description (Fig. 31). Small (30–35 µm diameter), freshwater, spherical, aloricate suctorian. Ectoparasitic on the exterior of the ciliate *Stokesia vernalis*. Capitate tentacles distributed all over surface of body. Spherical macronucleus, single marginal contractile vacuole. Reproduction by pseudo-scissiparity.

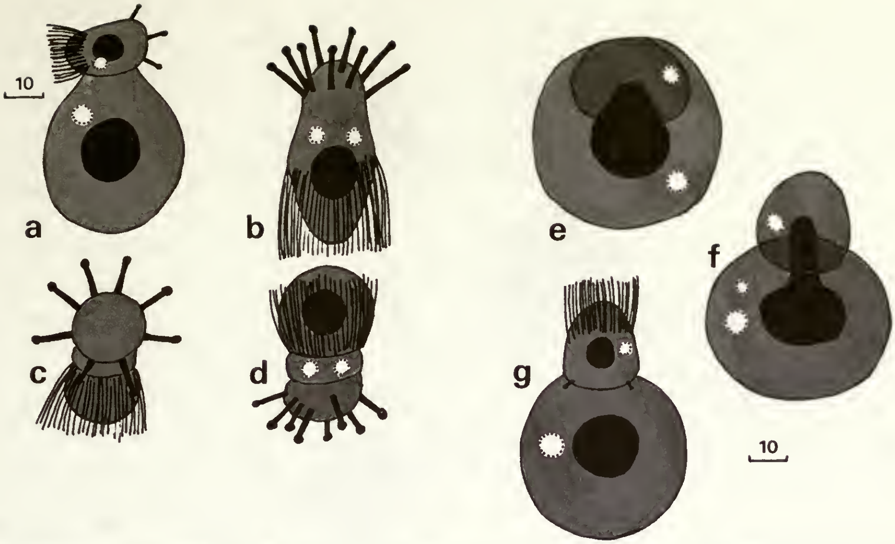

Fig. 30. *Podophrya stentoris:* (a–g) various stages in budding and embryos after Stein, 1867 (called *Sphaerophrya stentoris*).

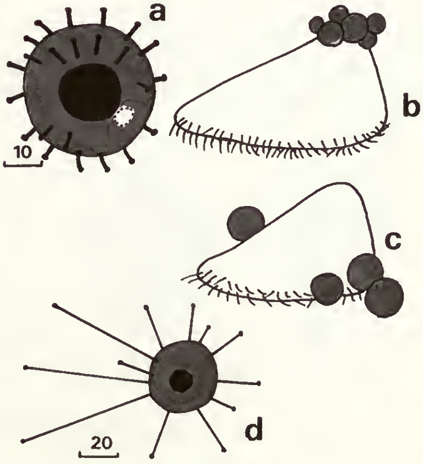

Fig. 31. *Podophrya stokesii:* (a) adult; (b,c) attached to host *Stokesia*; (d) adult. All after Mamaeva, 1979 (called *Sphaerophrya stokesii*).

Podophrya urostylae (Maupas, 1881) Jankowski, 1963

Sphaerophrya urostylae Maupas, 1881
Sphaerophrya stylonychiae Kent, 1882
Podophrya stylonychiae Foissner, 1980

Description (Fig. 32). Small (30–40 µm diameter), freshwater, spherical, aloricate suctorian. Free-living or endoparasitic in hypotrichous ciliates such as *Urostyla grandis* and *Stylonychia*. Few short capitate tentacles distributed all over surface of body. Central spherical macronucleus, single marginal contractile vacuole. Adult also able to live outside host when it is attached to inanimate objects by means of a stalk. Reproduction by pseudo-scissiparity. Buds ciliated by about six closely packed longitudinal rows of cilia and there are several rudimentary tentacles distributed over the bud. Stalked cyst, approximately ovoid with 4 or 5 transverse ridges.

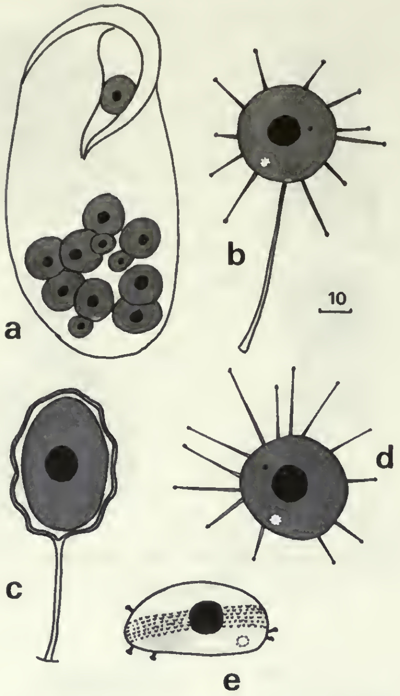

Fig. 32. *Podophrya urostylae:* (a) adults inside host *Urostyla;* (b–e) adult, cyst, adult without stalk and embryo respectively. All after Jankowski, 1963.

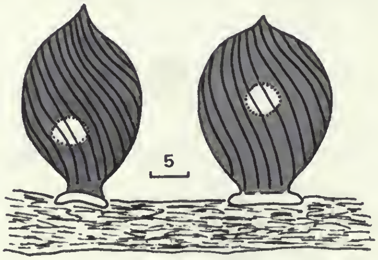

Fig. 33. *Podophrya tortuosa* cysts after Dons, 1918.

Dubious Species

Podophrya tortuosa Dons, 1918

DESCRIPTION (Fig. 33). Small (25 µm long), marine organism that is potentially a suctorian. Only the cyst has been described and for that reason it cannot be certain that it is ciliate of any kind. Cyst ovoid, anterior pointed, posterior flattened with a rim by which it is attached to the marine polychaete worm *Spirorbis*. Cyst striated obliquely. Single contractile vacuole.

Genus ***PARAPODOPHRYA*** Kahl, 1931

While members of this genus are superficially similar to certain species of *Podophrya* there is a fundamental character that separates the two genera. In *Parapodophrya* an elongated bud carrying an anterior corona of transverse ciliary rows develops by pseudo-scissiparity which is quite unlike anything produced by *Podophrya*. Furthermore all *Parapodophrya* species are free-living since no parasitic podophryid capable of producing the typical *Parapodophrya* bud has been described. In some cases the tentacles may widen towards their bases but this should not be regarded as evidence on its own that the species in question is a member of the above genus. However in most other respects the two genera resemble each other quite closely since their modes of reproduction, cysts and abilities for total transformation into a free-swimming bud-like state are similar.

Diagnosis of *Parapodophrya*

Fresh to brackish-water suctorians whose outline shape is typically spherical. Lorica absent, some species borne upon a stalk but this may often be absent. Free-living, usually attached to aquatic vegetation or inanimate objects. Never parasitic. Tentacles capitate and frequently widen markedly towards their base which may give body a serrated to star-like appearance. Tentacles distributed all over body, not in fascicles. Actinophores absent. The only cyst that has been described is stalked and heavily ribbed. Reproduction by pseudo-scissiparity, buds ciliated by a corona of several transverse rows of cilia. Bud typically elongated, wider at the anterior end that bears the ciliary rows. Some buds with rudimentary tentacles in the posterior body half. Whole cell may convert into a motile bud-like state.

Key to Species of *Parapodophrya*

1	Tentacles noticeably widen at base	2
	Tentacles do not noticeably widen at base	4
2	Without stalk, bases of tentacles very wide giving body a star-like appearance	***P. sparganium***
	With stalk, tentacle bases only moderately wide	3
3	Macronucleus spherical, zooid spherical	***P. soliformis***
	Macronucleus lemon-shaped, zooid pyriform	***P. palmigera***
4	Tentacles simply capitate	5
	Tentacle ends broadly spatulate	***P. typha***
5	Zooid covered in short denticle-like projections	***P. denticulata***
	Zooid without surface projections	6
6	With stalk	***P. soliformis***
	Without stalk	***P. nigricans***

Species descriptions of *Parapodophrya*

Parapodophrya soliformis (Lauterborn, 1908) Kahl, 1931

Sphaerophrya sol Lauterborn, 1901 *non* Mechnikov, 1864
Sphaerophrya soliformis Lauterborn, 1908
Podophrya soliformis Penard, 1918

DESCRIPTION (Fig. 34). This the type species is a small to medium (40–100 µm diameter), freshwater, spherical, aloricate suctorian. Capitate tentacles numerous, projecting from all over body surface, fine at the tips and widening towards their bases giving the cell surface a rather serrated appearance. Free-living, usually borne upon a stalk that is at least as long as the body diameter. Stalk joins body via a short cytoplasmic projection. Central spherical macronucleus, single contractile vacuole slightly eccentric. Reproduction by pseudo-scissiparity producing a ciliated embryo which has a corona of several transverse kineties near to the anterior end of the cell and sometimes a few rudimentary tentacles behind the cilia. Similar ciliated larvae can be produced by the total transformation of the adult. Spherical cyst with four transverse ribs, borne upon short stalk.

NOTE. This species has been the subject of several papers including Penard (1920) and Kormos (1960) in addition to those given above.

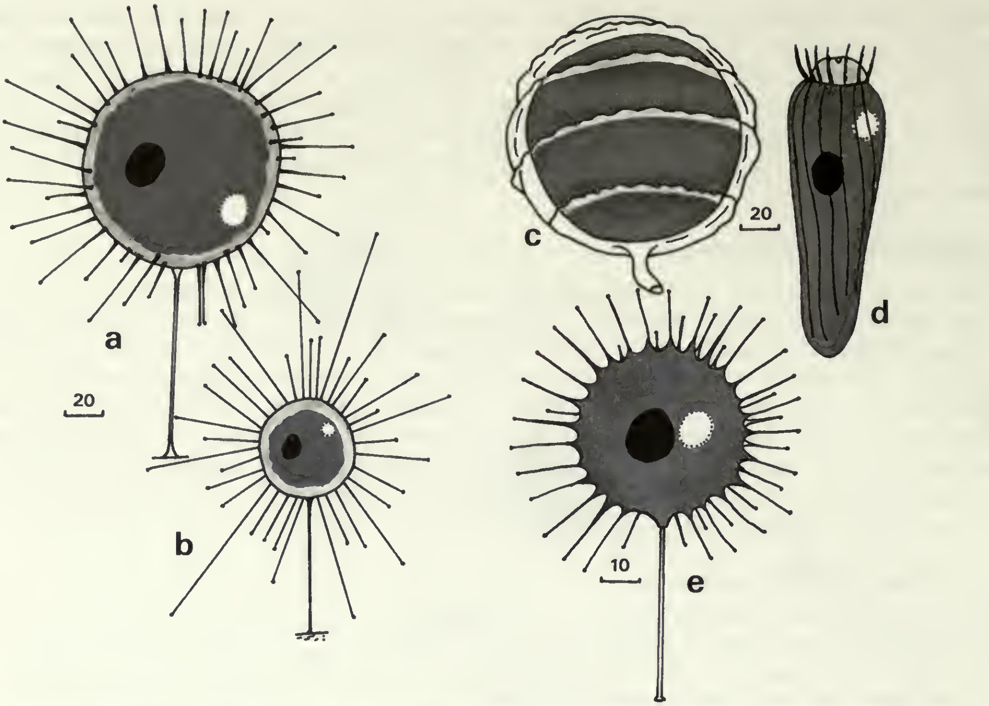

Fig. 34. *Parapodophrya soliformis:* (a,b) adults after Kahl, 1931 (called *Podophrya soliformis*); (c–e) cyst, embryo and adult after Penard, 1920 (called *Podophrya soliformis*).

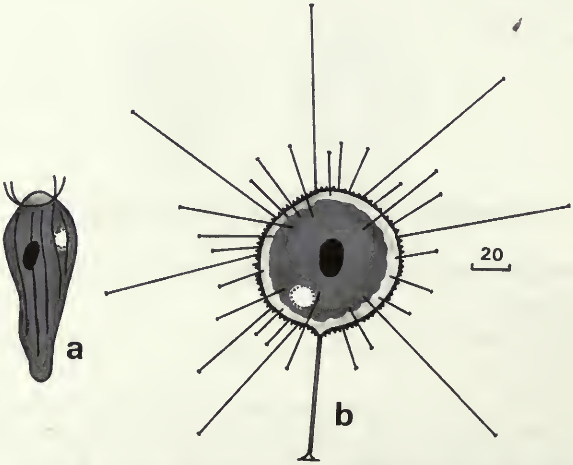

Fig. 35. *Parapodophrya denticulata:* (a,b) embryo and adult after Kahl, 1931.

Parapodophrya denticulata Kahl, 1931

Description (Fig. 35). Medium (70 µm diameter), freshwater to brackish, spherical, aloricate suctorian. Capitate tentacles numerous, projecting from all over body surface which is covered in short projections giving the cell surface a rather serrated appearance. Free-living, usually borne upon a stalk that is at least as long as the body diameter. Stalk joins body via a short cytoplasmic projection. Central ovoid macronucleus, single marginal contractile vacuole. Reproduction by pseudo-scissiparity producing an elongated ciliated embryo which has a corona of several transverse kineties near to the anterior end of the cell. Feeds on the ciliate *Spirostomum teres*.

Parapodophrya nigricans Kahl, 1931

DESCRIPTION (Fig. 36). Small to medium (50–60 µm diameter), freshwater to brackish, spherical, aloricate suctorian. Long capitate tentacles numerous, projecting from all over body surface. Free-living, not usually borne upon a stalk, body surface smooth. Central spherical macronucleus, single marginal contractile vacuole. Reproduction by pseudo-scissiparity producing an elongated ciliated embryo which has a corona of several transverse kineties near to the anterior end of the cell. Feeds on the ciliate *Prorodon ovum*.

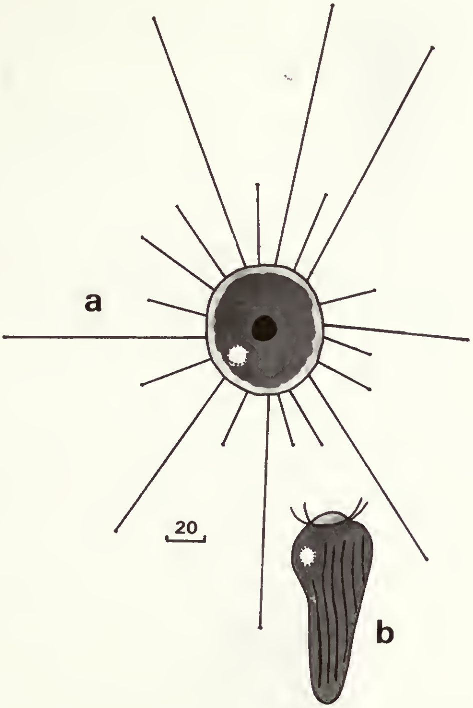

Fig. 36. *Parapodophrya nigricans:* (a,b) adult and embryo after Kahl, 1931.

Parapodophrya palmigera (Penard, 1920) n. comb.

Podophrya palmigera Penard, 1920
Podophrya comosa Penard, 1920

DESCRIPTION (Fig. 37). Medium (50–60 µm diameter), freshwater, pyriform, aloricate suctorian. Capitate tentacles numerous, projecting from all over body surface, fine at the tips and widening slightly towards their bases giving the cell surface a rather spiky appearance. Free-living, borne upon a stalk that is at least as long as the body diameter. Body projects out posteriorly at junction of stalk. Macronucleus eccentric, characteristically lemon-shaped, single marginal contractile vacuole. Reproduction by pseudo-scissiparity producing an elongated ciliated embryo which has a corona of several transverse kineties near to the anterior end of the cell.

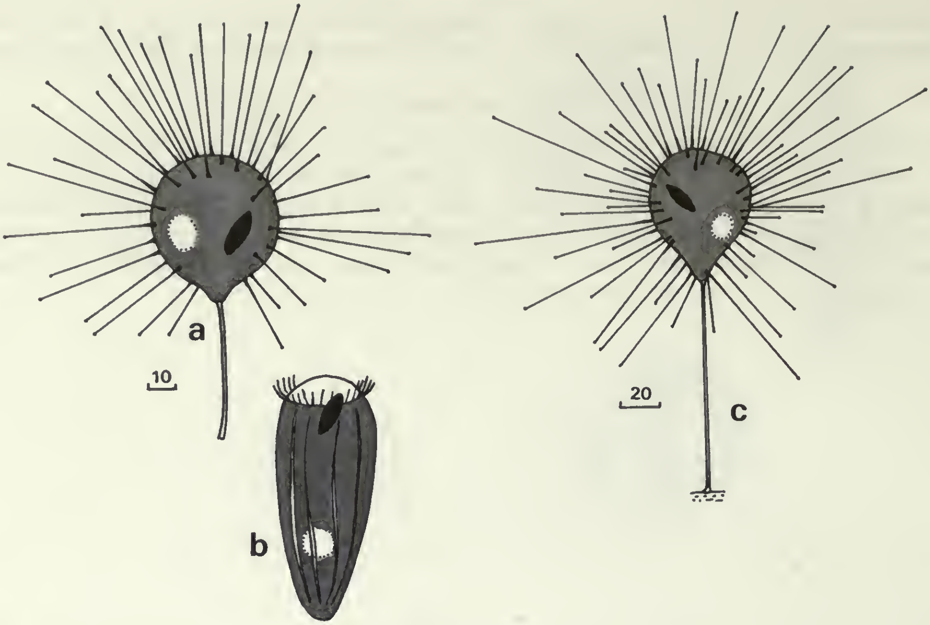

Fig. 37. *Parapodophrya palmigera*: (a,b) adult and embryo (called *Podophrya palmigera;* (c) adult (called *Podophrya comosa*). All after Penard, 1920.

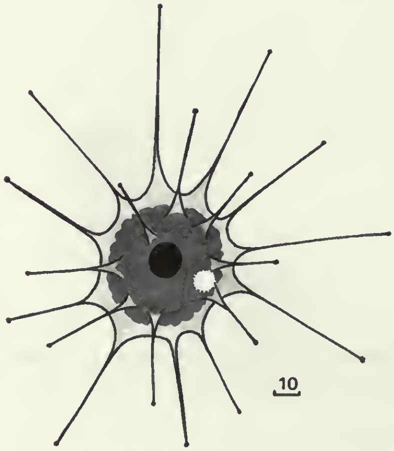

Fig. 38. *Parapodophrya sparganium* after Kahl, 1931.

Parapodophrya sparganium Kahl, 1931

DESCRIPTION (Fig. 38). Medium (50–60 µm diameter), brackish water, irregularly spherical, aloricate suctorian. Capitate tentacles numerous, projecting from all over body surface, fine at the tips and widening considerably towards their bases giving the cell surface a star-like appearance. Free-living, stalk absent. Central spherical macronucleus, single marginal contractile vacuole. Reproduction by pseudo-scissiparity producing an elongated ciliated embryo which has a corona of several transverse kineties near to the anterior end of the cell.

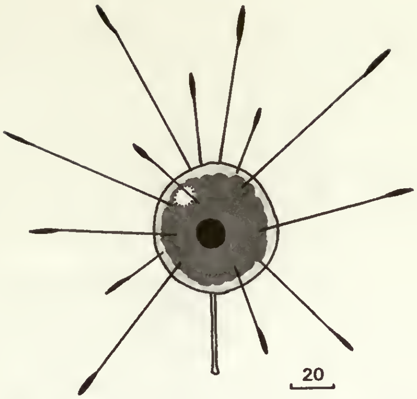

Fig. 39. *Parapodophrya typha* after Kahl, 1931.

Parapodophrya typha Kahl, 1931

Description (Fig. 39). Medium (50–60 µm diameter), freshwater to brackish, spherical, aloricate suctorian. Tentacles with spatulate spear-like ends, projecting from all over body surface. Free-living, usually borne upon a stalk that is almost as long as the body diameter. Body surface smooth. Central spherical macronucleus, single marginal contractile vacuole. Reproduction by pseudo-scissiparity producing an elongated ciliated embryo which has a corona of several transverse kineties near to the anterior end of the cell.

Genus *MUCOPHRYA* Gajewskaja, 1933

This single species genus closely resembles some of the stalkless species of *Podophrya* and perhaps will eventually become submerged in that genus. However the description of budding is not sufficiently detailed to positively identify it as pseudo-scissiparity or as simple exogenous budding and until that feature is elucidated it should remain as a separate genus. The possession of a thick mucous coat is not in itself thought to be sufficient to sustain its separate generic status since this is possibly a recent adaptation to the planktonic way of life. The saucer-shaped lorica is rather different from other podophryid cysts and this feature tends to strengthen the case for retaining it as a separate genus.

Diagnosis of *Mucophrya*

Freshwater suctorian whose outline shape is irregular, triangular to heart-shape. Lorica absent but there is a thick layer of mucous covering the only species described to date. Stalk absent. Free-living, planktonic, never parasitic. Tentacles capitate and retractile, distributed all over body, not in fascicles. Actinophores absent. Cyst saucer-shaped with frilled edge, cytoplasmic portion reduced, spherical lying centrally within cyst. Reproduction by exogenous buds.

Key to species of *Mucophrya*

1 Planktonic, covered in thick layer of mucous .... ***M. pelagica***

Species description of *Mucophrya*

Mucophrya pelagica Gajewskaja, 1933

Description (Fig. 40). Medium (65–110 µm diameter), freshwater, irregular heart-shape to triangular, aloricate suctorian. Tentacles capitate, projecting out from all over body surface, retractile. Free-living, planktonic, without stalk. Body covered in thick mucilaginous coat.

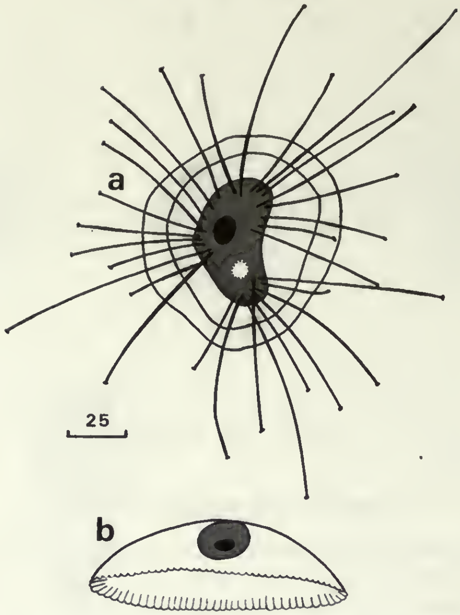

Fig. 40. *Mucophrya pelagica:* (a) adult; (b) cyst. Both after Gajewskaja, 1933.

Central ovoid macronucleus, two micronuclei, single marginal contractile vacuole. Reproduction by exogenous buds. Cyst saucer-shape, up to 130 µm in diameter, with a frilled edge. Cytoplasm in cyst centrally positioned and spherical.

Note. So far only recorded from Lake Baikal.

References

Batisse, A. 1975. Propositions pour une nouvelle systématique des Acinétiens (Ciliophora, Kinetofragminophora, Suctorida). *Compte Rendu Hebdomadaire des Séances de l'Academie des Sciences, Paris* (Ser. D) **280:** 1797–1800.

Bory, St. Vincent de. 1825 (1824). *Encyclopedie Methodique. Zoologie. Histoire Naturelle des Zoophytes, ou Animaux Rayonnes.* pp. 819, Paris, Agasse.

Buck, E. 1884. Ueber die ungestielte Varietat der *Podophrya fixa* Ehrg. *Bericht uber die Senckenbergischen Naturforschen Gesellschaft. Frankfurt a.M.* **1884:** 298–304.

Bütschli, O. 1887–1889. Protozoa. Abt III. Infusoria und System der Radiolaria. *In* Bronn, H. G. (Ed.), *Klassen und Ordnung des Thiersreichs* Vol. **1**, pp. 1098–2035. Leipzig, C. F. Winter.

Calkins, G. N. 1902. Marine protozoa from Woods Hole. *Bulletin of the United States Fish Commission. Washington* **21** (yr 1901): 413–468.

Canella, M.F. 1957. Studi i ricerci sui tentaculiferi nel quadro nella biologia generale. *Annali nell'Universita di Ferrara* **1:** 259–716.

Claparède, E. & Lachmann, J. 1859. Études sur les infusoires et les rhizopodes. *Mémoires de l'Institut National Genèvois. Genève* **6** (yr 1858): 261–482.

Clement, F. 1967. Sur une *Sphaerophrya* (Cilie) ectoparasite des *Euplotes*. *Hydrobiologia* **29:** 245–255.

Clement-Iftode, F. 1967. Sur une *Sphaerophrya* ectoparasite de *Nassula elegans*. *Protistologica* **3:** 127–132.

Collin, B. 1911. Étude monographique sur les Acinétiens I. Recherches expérimentales sur l'étendue des variations et les facteurs tératogènes. *Archives de Zoologie Expérimentale et Génerale. Paris* **8:** 421–497.

Collin, B. 1912. Étude monographique sur les Acinétiens II. Morphologie, Physiologie, Systématique. *Archives de Zoologie Expérimentale et Génerale. Paris* **51:** 1–457.

Corliss, J.O. 1979. *The Ciliated Protozoa: Characterization. Classification and Guide to the Literature* 2nd edition, Pergamon Press, Oxford, 455 pp.

Curds, C.R. 1985*a*. A revision of the Suctoria (Ciliophora, Kinetofragminophora) 1. *Acineta* and its morphological relatives. *Bulletin of the British Museum (Natural History). Zoology, London* **48:** 75–129.

Curds, C.R. 1985*b*. A revision of the Suctoria (Ciliophora, Kinetofragminophora) 2. An addendum to *Acineta. Bulletin of the British Museum (Natural History). Zoology, London* **49:** 163–165.

Curds, C.R. 1985*c*. A revision of the Suctoria (Ciliophora, Kinetofragminophora) 3. *Tokophrya* and its morphological relatives. *Bulletin of the British Museum (Natural History). Zoology, London* **49:** 167–193.

Dieckmann, J. 1985. *Podophrya grelli* n.sp., ein wirtsspezifisches Suktor, parasitierend auf *Stylonychia lemnae* Ammerman und Schlegel, 1983. *Archiv für Protistenkunde. Jena* **129:** 155–170.

Dingfelder, J.H. 1962. Die Ciliaten vorubergerehender Gewasser. *Archiv für Protistenkunde. Jena* **105:** 509–658.

Dons, C. 1918. Neue marine Ciliaten und Suctorien. *Tromso Museums Aarshrifter* **38–39** (yr 1915–16): 75–100.

Dujardin, F. 1841. *Histoire Naturelle des Zoophytes. Infusoires* De Fain et Thunot, Paris. 678 pp.

Ehrenberg, C.G. 1833. Dritter Beitrag zur Erkenntnis grosser Organisation in der Richtung des Kleinsten Raumes. *Abhandlungen der Akademie der Wissenschaften der DDR. Berlin* yr **1835:** 145–336.

Engelmann, T.W. 1878. Ueber Entwicklung und Fortpflanzung der Infusorien. *Morphologisches Jahrbuch. Leipzig* **1:** 573–635.

Fauré-Fremiet, E. 1945. *Podophrya parasitica* nov. sp. *Bulletin Biologique de la France et de la Belgique* **79:** 85–97.

Florentin, R. 1899. Études sur la faune des mares salées de Lorraine. *Annales des Sciences Naturelles. Paris.* Zoologie **9:** 209–349.

Foissner, W. 1980. Taxonomische Studien uber die Ciliaten des Grossgbecknergebetes (Hohe Tauern, Osterreich). IV Familien Spathidiidae, Podophryidae und Urnulidae. *Verhandlungen der Zoologisch-Botanischen Gesellshaft in Wien* **118/119:** 97–112.

Fukui, T. & Morishita, I. 1962. About suctoria in activated sludge. *Tansui-Seibutsu (Freshwater Organisms)* **8:** 3–7.

Gajewskaja, N. 1933. Zur Oekologie, Morphologie und Systematik der Infusorien des Baikalsees. *Zoologica. Stuttgart* **32:** 1–298.

Ghosh, E. 1929. Two new suctoria from sewer water. *Journal of the Royal Microscopical Society. London* **49:** 222–223.

Gonnert, R. 1935. Uber Systematik, Morphologie, Entwicklungsgeschichte und Parasiten einiger Dendrosomidae nebst Beschreibung zweier neuer Suktorien. *Archiv fur Protistenkunde. Jena* **86:** 113–154.

Gourret, P. & Roeser, P. 1886. Les Protozoaires du Vieux-Port de Marseille. *Archives de Zoologie Expérimentale et Génerale. Paris* **4:** 443–534.

Greef, R. 1889 (1888). Studien uber Protozoen. *Sitzungsberichte der Gesellschaft zur Beforderung der Gesamten Naturwissenschaften zu Marburg* **1888:** 90–158.

Guilcher, Y. 1951. Contributions à l'étude des ciliés gemmipares, Chonotriches et Tentaculifères. *Annales des Sciences Naturelles. Paris* (Zool) **13:** 33–132.

Hammann, I. 1952. Okologische und biologische Untersuchungen an Susswasserperitrichen. *Archiv fur Hydrobiologie. Stuttgart* **47:** 177–228.

Holm, F. 1925. Ueber die Suktorien in dr Elbe bei Hamburg ind Lebensbdungen. *Archive fur Hydrobiologie. Stuttgart* **4:** 389–440.

Jankowski, A.V. 1963. (Pathology of Ciliophora II. Life cycles of suctoria parasitising in *Urostyla* and *Paramecium*—in Russian). *Tsitologiya. Leningrad* **5:** 428–439.

Jankowski, A.V. 1967. (New genera of tentacled Infusoria (Suctoria)—in Russian). *Materialy V Konferentsii uch Moldavii Zoologicheskii* p. 35: 6.

Jankowski, A.V. 1973. (Suctorian infection in *Bursaria truncatella* OFM—in Russian) *Parazitologiya* **7:** 401–406.

Jankowski, A.V. 1981 (New species, genera and families of tentacled Infusoria (class Suctoria)—in Russian). *Trudy Zoologicheskogo Instituta. Akademiya Nauk SSSR. Leningrad* **107:** 80–115.

Jankowski, A.V. 1982. (New genera of protozoan symbionts for the fauna of Lake Baikal—in Russian) in G.I. Galazii ed. (New data on the fauna of Lake Baikal, Part 3—in Russian). *Izdalelistvo 'Nauka' Sibirskoe otdelenie Novosibirsk* p. 25–32.

Kahl, A. 1931. Uber die verwandtschaftlichen Beziehungen der Suktorien zu den prostomen Infusorien. *Archiv fur Protistenkunde. Jena* **73:** 423–481.

Kahl, A. 1934. Suctoria *in* Grimp G. & Wagler E. (Eds.) *Die Tierwelt der Nord und Ostsee* Bd. 1. (Teil II c5): 184–226.

Kellicott, D.S. 1887. Notice of some freshwater infusoria, with remarks on collecting and preserving these delicate animals. *Microscope. Detroit* **7:** 225–233.

Kent, W.S. 1880–1882. *A Manual of the Infusoria* vols I–III: pp. 913, London, David Bogue.

Kormos, K. 1960. The formation of the swarmer of *Parapodophrya* and its relationship. *Journal of Protozoology* 7, Suppl: 22.

Lachmann, J. 1859. Sitzungsberichte vom 6 Juli 1859. *Verhandlungen des Naturhistorischen Vereins der Preussischen Rhienlande und Westfalens. Bonn* **16:** 91–94.

Lauterborn, R. 1901. Die 'sapropelische' Lebewelt. *Zoologischer Anzeiger. Leipzig* **24:** 50–55.

Lauterborn, R. 1908. Protozoen-Studien. V. Zur Kenntniss einiger Rhizopoden und Infusorien aus dem Gebeite des Oberrheins. *Zeitschrift fur Wissenschaftliche Zoologie. Leipzig* **90:** 645–669.

Mamaeva, N.V. 1979. (*Infusoria of the Volga Basin. An ecological outline.—in Russian)* Nauka, Leningrad. 148 pp.

Maupas, E. 1876. Sur l'organisation et le passage à l'état mobile de la *Podophrya fixa. Archives de Zoologie Expérimentale et Générale. Paris* **5:** 401–428.

Maupas, E. 1881. Contribution à l'étude des Acinétiens. *Archives de Zoologie Expérimentale et Génerale. Paris* **9:** 299–368.

Mechnikov, E. 1864. Ueber die Gattung *Sphaerophrya. Archiv fur Anatomie und Physiologie. Leipzig* **1864:** 258–261.

Muller, O.F. 1786. *Animalcula Infusoria Fluviatilia et Marina.* 367 pp. Havniae et Lipsiae.

Penard, E. 1918. Sur un Tentaculifère peu connu, *Podophrya soliformis* (Lauterborn). *Revue Suisse de Zoologie. Genève* **26:** 1–16.

Penard, E. 1920. Étude sur les Infusoires Tentaculifères. *Mémoires de la Societe de Physique et d'Histoire Naturelle de Genève* **39:** 131–227.

Perty, M. 1852. *Zur Kenntniss Kleinster Lebensformen nach Bau. Funktionem. Systematik mit Specialverzeichneiss der in der Schweiz Beobacteten.* Jent u. Reinert, Bern. 228 pp.

Sand, R. 1896. Les Acinétiens d'eau douce. *Annales de la Societé Belge de Microscopie. Bruxelles* **20:** 7–12: 85–103.

Sand, R. 1899–1901. Étude monographique sur le groupe des Infusoires Tentaculifères. *Annales de la Societé Belge de Microscopie* **24:** 57–189 **25:** 1–204.

Schewiakoff, W. 1892. Ueber die Geographische Verbreitung der Susswasser-Protozen. *Zapiski Akademii Nauk SSSR. Leningrad* (Ser. 7) **41:** 1–201.

Simmons, W. J. 1889. Note on a species of *Podophrya* found in Calcutta. *The American Monthly Microscopical Journal. Washington* **10:** 145–146.

Spencer, C.S. 1917. Observations on the Protozoa with descriptions and drawings of some probable new species. *Proceedings of the Iowa Academy of Sciences. Des Moines* **24:** 335–351.

Stein, F. 1854. *Die Infusionsthiere auf ihre Entwickelungsqeschichte untersucht* pp. 265. Leipzig.

Stein, F. 1867. *Der Organismus der Infusionsthiere nach eingenen Forschungen in Systematischer Reihenfolge bearbeit* II: pp. 355. Leipzig.

Stokes, A.C. 1885. Notices of new freshwater Infusoria. *American Monthly Microscopical Journal. New York* **6:** 183–190.

Strouhal, H. 1939. Die in den Hohlen von Warmbad Villach, Karnten, festgestelten Tiere. *Folia Zoologica et Hydrobiologica. Herausgegeben von E. Strand. Riga* **9:** 247–290.

Weisse, J.F. 1847. Verzeichniss von 155 in St. Peterbourg beobachteten Infusorienarten. *Bulletin de L'Academie Imperiale des Sciences de St. Petersbourg* **5:** 39–47.

Zacharias, O. 1893. Faunistische und biologische Beobachtungen am Gr. Ploner See. *Forschungsberichte aus der Biologischen Station zu Plon. Berlin* **1:** 1–52.

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The Identity of *Cribrilaria innominata* (Couch, 1844) (Bryozoa, Cheilostomata)

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Synopsis

The universally accepted identity of *Lepralia innominata* Couch, 1844, i.e. that of a cribrilinid species commonly placed in the genus *Cribrilaria,* was established by Johnston in the second edition (1847) of *A History of the British Zoophytes* but may not have been that intended by Couch. In the absence of the type series, from which the true nature of the species might have been determined, Johnston's concept of the taxon is accepted and a neotype is selected from his material. A redescription based on the neotype is given. It is hoped thereby to restrict and stabilise the usage of the name, which has been applied to a number of Recent and fossil cribrilinid species. The occurrence of the species as a fossil in the European Neogene is regarded as unproven; a record from the Pliocene Crags of eastern England is specifically rejected.

Introduction

Studies in the last few years have revealed considerable present-day diversity within the cribrimorph genus *Cribrilaria,* particularly in the NE. Atlantic region (Harmelin, 1970; 1978; 1984). This realisation has accompanied a narrowing of species concepts within the genus, necessitating a re-examination of the commonly-cited older nominal species in order to establish their precise identity. Following the view of Hincks (1880), *Cribrilaria innominata* (Couch, 1844) was regarded by many workers as merely a form or variety of *C. radiata* (Moll, 1803). Recently, however, the separate identity of the two species has been reaffirmed, for instance by Harmelin (1970) and Hayward & Ryland (1979). The apparent intergradation exhibited by *C. radiata* and *C. innominata* seems to have resulted, at least in part, from the confusion of several species under each name. A neotype of *C. radiata* was selected by Harmelin (1970) who also distinguished two forms, A and B, of *C. innominata.* Harmelin attributed a relatively restricted geographical distribution (perhaps exclusively Mediterranean) to *C. radiata*, but regarded *C. innominata* as cosmopolitan. Gordon (1984) also considered *C. innominata* to be cosmopolitan. However, type material of *C. innominata* has not been recognised, and it seems highly probable that the name is still being used for several different but related species. The present paper is an attempt to examine the origin of the concept of *Cribrilaria innominata* and to clarify its identity by reference to type material.

Development of the concept of *C. innominata*

The original description and figure (R. Q. Couch, 1844) of *Lepralia innominata* are inadequate to define the species. There is, indeed, little to suggest a cribrimorph identity for the taxon. Couch did not place any other taxon in synonymy with his new species. The provenance of his material was given as 'On stones, rare. Goran, *Mr. Peach*. Polperro. Mount's bay' (Couch, 1844: 114). Charles W. Peach's assistance in providing specimens for Part 3 of *A Cornish Fauna* was warmly acknowledged by Richard Couch (1844; iv–v, preface dated August 1844). Peach worked as a Customs Officer in Cornwall; from October 1834 to March 1845 he was based at Goran (or Gorran) Haven, south of Mevagissey, then he moved to Fowey before transfer to Scotland in December 1849 (Boase & Courtney, 1878; Lee, 1895).

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Peach himself announced the discovery of two new species of *Lepralia* to a meeting of the British Association for the Advancement of Science, at York in September 1844. The published summary of his communication (Anon., 1845: 65) cited these as '*Lepralia catenata* and *Lepralia pectinata,* which [Peach had stated] Dr. Johnston of Berwick-on-Tweed and Mr. Couch of Penzance have pronounced new and good species'. No descriptions or figures were given and, if this report (in the third person, by an anonymous editor) of his remarks qualifies as a publication of the names by Peach, they must be regarded as *nomina nuda.* The report of the Royal Institution of Cornwall for 1845 lists donations to their Museum for the period 3 December 1844 to 7 November 1845. These included specimens of 18 species of coelenterates and bryozoans from Goran and Fowey Harbour presented by Peach; amongst them were *Lepralia catenata* and *L. pectinata,* but not *L. innominata.* (*L. catenata* was *Chorizopora brongniartii* (Audouin) according to later authors. *L. pectinata* will be discussed below.) Peach's donation did not include material referred to any of the new species described by Couch (1844). None of Peach's bryozoan specimens are now to be found in the collections of the Royal Institution of Cornwall (R. D. Penhallurick, Assistant Curator, pers. comm., 1985).

Johnston (1847) redescribed *Lepralia innominata* in his *History of the British Zoophytes.* In the preface to this work (i.e. to the second edition) he acknowledged the assistance of both Peach and Couch. However, Peach's name alone was placed after the diagnosis of *L. innominata*, the significance of this convention being explained by Johnston (1847: 30, footnote) as follows: 'The name affixed to the specific character is that of the person who, so far as I have been able to ascertain the fact, added the species to the British Fauna'. Johnston placed 'Lep. pectinata, *Peach* MS' in synonymy with *L. innominata*; his listed material of the species was provided by Peach from Cornwall and by G. C. Hyndman from W. Scotland. Johnston's diagnosis, description and figure (1847: 319–320 and pl. 55 fig. 12) appear to contradict those of Couch (1844: 114–115 and pl. 22 fig. 4) on several points. Thus 'cells short, sub-orbicular or ovate' (Johnston) contrasts with Couch's figure showing slender zooids about three times as long as broad (although Couch's own text also says 'oval'). Johnston states 'aperture ... armed with several short denticles or spines not longer than its diameter' (perhaps describing spine bases left after spines had been lost) whereas Couch indicates long oral spines clearly exceeding the dimensions of the orifice. Most significantly, Johnston specifies ridges on the zooids radiating from the midline, but Couch describes and illustrates a series of short, sub-parallel transverse bands. Perhaps not surprisingly, Johnston characterised Couch's figure (and description?) as 'very bad'. The cribrilinid concept of *L. innominata* adopted by later workers seems clearly to have been established by Johnston rather than Couch. However, Johnston's account is insufficient to allow the separation of one particular species from other, related, cribrimorphs.

A large collection, presented by Johnston to the British Museum in 1847, was described in the handwritten accessions book as 'The authentic specimens from which the descriptions in "Johnston's British Zoophytes" were taken'. Material of *L. innominata* from the locations listed by Johnston (1847) is represented by only two specimens: BM(NH) 1847.9.16.32 (Goran, Cornwall, C. W. Peach—a label with the specimen indicates that this was collected in September 1843) and 1847.9.16.122 (Sana Island, W. Scotland, G. C. Hyndman). These specimens are conspecific; they are both labelled *L. pectinata* in Johnston's handwriting. The collection included six additional specimens listed in the accessions book as *L. pectinata* (as were the two just mentioned), for which the locality was given simply as 'British'. This poorly localised material was not specifically referred to by Johnston (1847). Some of these specimens are conspecific with those from Cornwall and Scotland; others belong to a closely related (possibly conspecific) form of similar zooidal dimensions sharing the large suboral lacuna regarded as characteristic of *L. innominata* by later authors, but differing in details of the frontal wall calcification. The status of the latter form will not be further discussed here.

Busk (1854: pl. 86 fig. 2) illustrated *Lepralia innominata* from one of Johnston's specimens, 1847.9.16.32, collected at Goran Haven by Peach. This was the most detailed and informative figure of *L. innominata* yet published, clearly showing a distinct triangular area, proximal to the D-shaped orifice, pierced by a large suboral pore or lacuna. Busk's diagnosis of the species also noted this suboral pore. *Lepralia pectinata* Peach MS was listed in the synonymy for the species.

In addition, Busk provided a second figure of *L. innominata* (pl. 86 fig. 3). The illustrated specimen, 1847.9.16.79, was also part of Johnston's collection. However, there is no record that Johnston himself identified this colony as *L. innominata*. The colony encrusts a bivalve shell also colonised by several other species of bryozoan; Johnston's labels, and the accession details, refer to these other species only. The species illustrated in pl. 86 fig. 3 would today be placed in the genus *Puellina*; it agrees with the description by Hincks (1880: 186) of *Cribrilina radiata* var. *a*, which has been taken to be *Puellina setosa* (Waters).

Busk (1860: 282) later noted the possibility that *L. innominata* (referred to as '*L. innominata*, Johnst.') might be a synonym of *Eschara radiata* Moll, 1803, a species described from the Mediterranean Sea. Smitt (1873: 22–23) transferred both species to the genus *Cribrilina* but discounted the possibility of synonymy, giving 'the presence, on *Cribrilina innominata*, of a lunate pore in the triangular or semicircular space, proximally of the zooecial aperture' as a character distinguishing the two species.

Hincks (1880: 185) dismissed Couch's figure (and description?) as 'worthless' and followed Johnston (1847) and later authors in his concept of *Lepralia innominata*. Hincks regarded the species, referred to (1880: 187) as '*Lepralia innominata*, Johnston', as merely a form of *Cribrilina radiata* (Moll). His confusing account recorded both the '*radiata* form' and the '*innominata* form' from Britain. The two forms were considered to intergrade.

Peach (1882) updated the work of Couch (1844) by adding subsequent Cornish records and revising nomenclature with reference to Hincks (1880). *Lepralia innominata* Couch, 1844 was listed in synonymy with *Cribrillina radiata* (*lapsus pro Cribrilina*), thereby endorsing Hincks' treatment of the species. *L. pectinata* was not mentioned.

The genus *Cribrilaria* was founded by Canu & Bassler (1928; 1929: see Lagaaij, 1952) with *C. radiata* as type-species; it was regarded by Gordon (1984) as a sub-genus of *Puellina* Jullien, 1886.

From all this it is apparent that the accepted concept of *Cribrilaria innominata* may not be that intended by Couch (1844), but was established later by Johnston (1847) and partially clarified by Busk (1854) and Smitt (1873). Johnston apparently based his concept of the taxon on Peach's undescribed *Lepralia pectinata,* but treated this as a synonym of Couch's *L. innominata*. The source of Johnston's belief that *L. innominata* and *L. pectinata* were conspecific has not been ascertained. Peach reportedly checked the identity of *L. pectinata* as a new species with Couch during or before 1844 (Anon., 1845), but also provided part of the type material for *L. innominata*. The name *L. pectinata* was not mentioned by Couch (1844), but was apparently still being used by Peach and Johnston in a public talk and for the labelling of specimens around the time of publication of Couch's paper. Peach (1882) accepted Hincks' (1880) treatment of *L. innominata*, implying that he did not question the concept of the taxon that then prevailed.

Non-availability of original type material

A Cornish Fauna, of which Richard Couch's account of the 'zoophytes' formed Part 3, was subtitled 'Intended to form a Companion to the Collection in the Museum of the Royal Institution of Cornwall'; it was published in Truro by the Institution. Type material of *L. innominata* might therefore be sought in the Institution's Museum. In the faunal lists of Parts 1 and 2 (J. Couch, 1838; 1841), species represented in the Museum collection were marked with an asterisk. However, no such convention was adopted for Part 3. This may imply that little relevant material was present in the collection at the time. The present author has been unable to find any record in the Institution's Reports from 1829 to 1871 of the accession to their Museum of a substantial collection of 'zoophytes' that might have been the basis for Richard Couch's work. The Reports for this period include detailed lists of donations compiled approximately once a year; major purchases are noted in the body of the Report. Clear mention is made of material relating to Parts 1 and 2 (particularly in Reports for the years 1837, 1838, 1840 and 1850).

The collection of the Institution's Museum was moved to new buildings during 1917 and 1918. Some time before this move was scheduled to be completed, the former premises were commandeered by the Army Council and it was necessary to vacate the old building hurriedly (as detailed in the Report for 1918). Time did not permit the orderly relocation of the remaining collections, and a mass of material was stored in the basement of the new premises. Much of this material had not yet been unpacked when a flood destroyed it during the 1950s. None of Richard Couch's 'zoophyte' specimens are now to be found in the collection of the Institution (R. D. Penhallurick, Assistant Curator, pers. comm. to P. J. Chimonides, 1976 and to P. F. S. Cornelius, 1977). Any part of Couch's collection at the Royal Institution of Cornwall (if such a collection existed) that survived into the 1950s was apparently destroyed by the flood.

A second possible location for material studied by Couch would have been the small Museum of the Penzance Natural History and Antiquarian Society. Richard Couch lived in Penzance, and held the honorary post of Curator of the Museum from 1845 to 1855 (as shown by the Society's Reports). However, the Museum no longer exists, and its collections have been scattered and, in part, destroyed. No bryozoan collection attributable to R. Q. Couch is now to be found amongst material known to have been transferred from the Society's Museum, either to Penlee House Museum (Penzance) or elsewhere (Stella M. Turk, Biological Records Unit, Institute of Cornish Studies, pers. comm., 1985).

Couch did not mention *Lepralia innominata* in his subsequent papers. It is concluded that no recognisable type material of *L. innominata* survives.

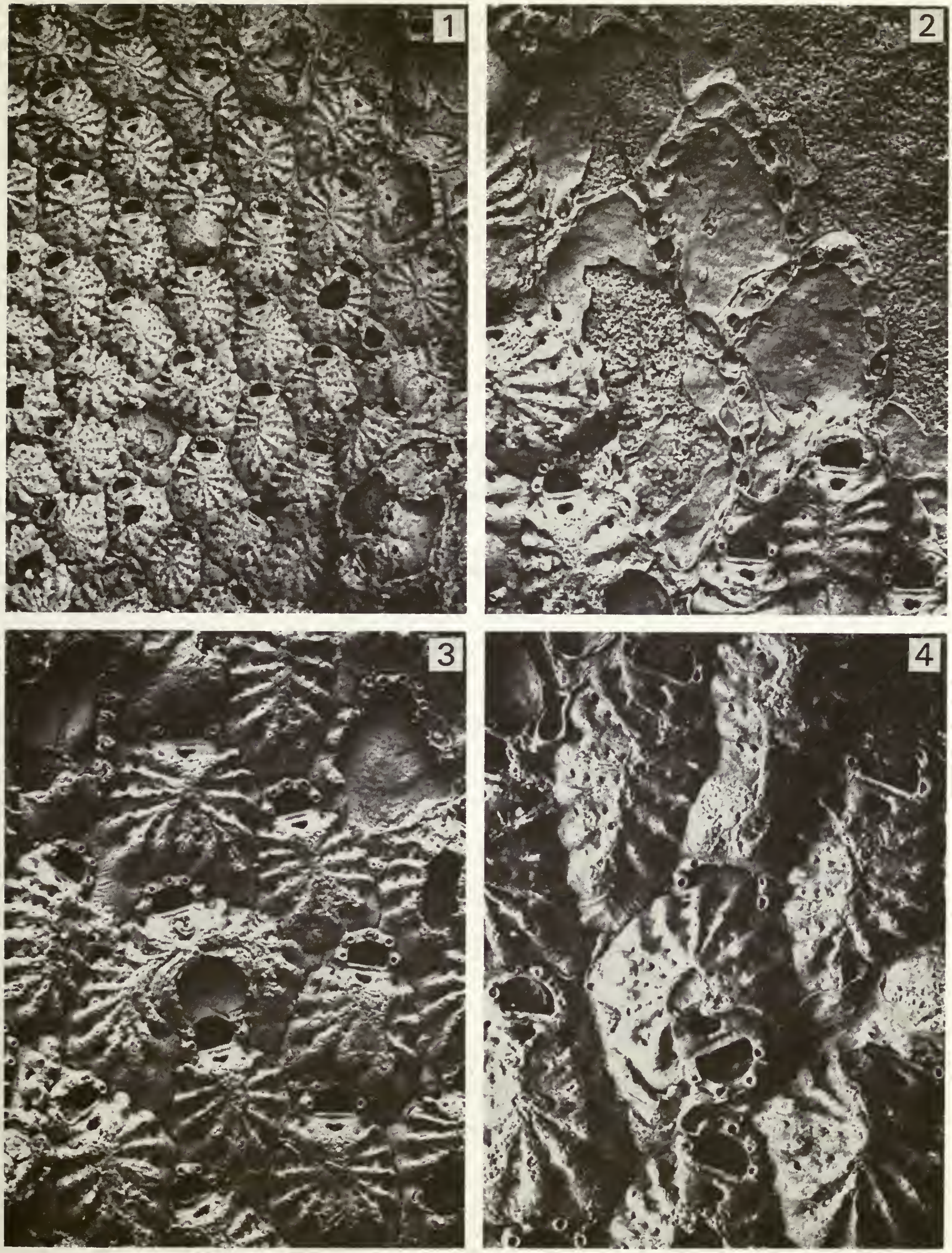
Selection of neotype

In the absence of material from the type series, there seems to be no hope that the true identity of Couch's taxon can ever be determined. The present paper therefore establishes a neotype for *Cribrilaria innominata* in accordance with accepted usage of the name. Since the specimen selected came from one of the type localities of Couch's species, was amongst those before Johnston (1847), and was one of those illustrated as *L. innominata* by Busk (1854), it is hoped thereby to ensure the stability of the name. The author is not aware that this choice of neotype results in any other nominal taxon passing into synonymy with *C. innominata*. A redescription of the species based on the neotype is provided in an attempt to define the species precisely and thus facilitate future revisory work.

The colony encrusting a shell registered as BM(NH) 1847.9.16.32 is selected here as the neotype of *Lepralia innominata* Couch, 1844; the specimen was part of the Johnston collection donated to the British Museum in 1847. Only two of the labels accompanying the specimen appear to pre-date its donation. They read: 'Goran. Sep. 1843 Lepralia pectinata' (with small sketch of two zooids) and '64d Lepralia pectinata' (with the BMNH registration number added in different handwriting). The first label was very probably written by C. W. Peach. The second is in Johnston's handwriting. The specimen is believed to be part of the material listed as *Lepralia innominata* by Johnston (1847); it was listed by Gray (1848: 121) as specimen 'a' of *L. innominata*; it was illustrated, again as *L. innominata*, by Busk (1854: pl. 86 fig. 2; *cf.* present paper, Fig. 1). The single colony, *c.* 5 × 5 mm, encrusts the inner (concave) surface of a broken *Venerupis pullastra* (bivalve mollusc) shell, close to its dorsal margin. It is situated between the tube of a serpulid polychaete (*Pomatoceros* sp.) and the colony of another cheilostome bryozoan, *Escharoides* sp., which was also illustrated by Busk (1854: pl. 88 fig. 5), as *Lepralia coccinea*. Many of the zooecial chambers of the cribrimorph are occupied by a folliculinid ciliate (Figs 7, 8), indicating that most or all of the colony was dead at the time of collection. The colony has *c.* 200 autozooids, of which *c.* 45 are ovicellate. There are five avicularia, three of which are badly damaged.

Redescription of *Cribrilaria innominata* based on the neotype

Colony encrusting, consisting of single layer of clearly delimited zooids. Frontal wall of autozooid convex in transverse section. Shape of autozooid in frontal view variable: often irregular-ovoid, sometimes broadly bifid proximally (with duplication of radiating pattern of costae) when



Figs 1–4 Scanning electron micrographs of *Cribrilaria innominata*, neotype (1847.9.16.32): (1) part of colony × 39, the left-central ovicellate zooid and those surrounding it being those illustrated by Busk (1854); (2) pore chambers visible in damaged zooids × 73; (3) proximally bifid zooid with duplication of radiating pattern of costae × 72; (4) regenerated zooid with oblique polarity axis × 105.

Table 1 Measurements on neotype, in mm, excluding periancestrular zooids

	Range	Mean	No. of Observns	Comments
Length of autozooid	0·35–0·53	0·44	30	Up to 0·63 if long proximal extension of gymnocyst present. (Measurement excluded ovicell if present.)
Width of autozooid	0·24–0·38	0·30	30	Up to 0·58 in proximally bifid zooids
Length of orifice	0·05	—	28	Rarely 0·06
Width of orifice	0·08–0·09	—	29	Rarely 0·10.
Length of ovicell	0·15–0·20	—	10	—
Width of ovicell	0·18–0·21	—	10	—

passing to either side of proximal zooid (Fig. 3). Exposed lateral gymnocyst narrow. Proximal gymnocyst more extensive, often forming narrow proximal extension(s) between neighbouring zooids. Pericyst (= costate frontal shield) with nine to 14 costae (most commonly 12; fewer in periancestrular zooids; up to 16 in proximally bifid zooids). Costae raised, distinct, each with steeply inclined basal portion bearing minute pelmatidium (Fig. 7); variably developed tubercle or short ridge borne at angle of basal portion of costa and more shallowly inclined subsequent portion. Pericyst with blunt suboral median mucro passing into variably developed median ridge. One to three (? rarely four) very small intercostal pores between successive costae; additional single larger pore, with distinct lip along basal margin, between bases of successive costae.

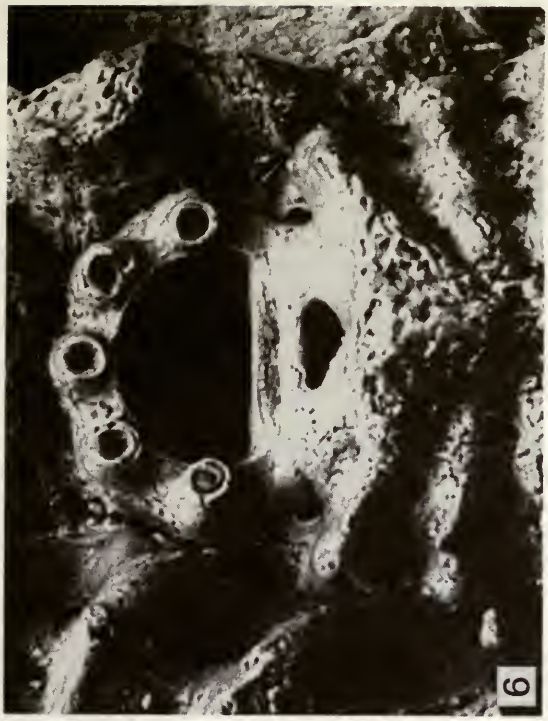
Orifice (Fig. 6) D-shaped, broader than long, proximal edge straight. Five evenly-spaced spine-bases around lateral and distal margin of orifice in non-ovicellate autozooids (only four in one regenerated zooid, Fig. 4). Ovicellate zooids with two closely-spaced spine bases on each side of orifice (the more distal sometimes partially obscured by ovicell). Strongly inclined triangular area between orifice and umbo (not included in counts of costae given above), pierced by large lacuna of variable shape. Each autozooid with three or four pairs of distolateral pore chambers plus one distal pore chamber (? sometimes double) (Fig. 2). Uncalcified external openings of pore chambers (seen in zooids on edge of colony) relatively large, as wide as or wider than calcification separating them.

Ovicell roughly globular, often partially embedded in distal autozooid, with variably developed low ridges or elongate tubercles in more or less radiating pattern on frontal surface, but no pores; median suture line sometimes discernible (Fig. 5). Avicularium (Figs 7, 8) interzooidal, without pivotal bar; rostrum elongate-triangular, edges converging towards tip at angle of *c.* 25–30°, slightly raised (i.e. neither closely adpressed to frontal wall of adjacent autozooid nor lying along interzooecial sulcus). Combined length of palate and frontal non-calcified area *c.* 0·17 mm (two measurements only); proximal gymnocyst of avicularian chamber clearly shorter than this. Ancestrula obscured.

Discussion

Successive generations of bryozoologists have shown a remarkable willingness to indulge in debate on the status and identity of *Lepralia innominata* without pausing to define the species adequately by reference to type material. As a result, many of the numerous records in the

Figs 5–8 Scanning electron micrographs of *Cribrilaria innominata*, neotype (1847.9.16.32): (5) part of colony viewed at angle to emphasise surface sculpture ×72; (6) orifice of autozooid ×350; (7) avicularium and adjacent autozooids ×137, arrows indicate pelmatidia; (8) avicularium (same zooid as Fig. 7) ×230, arrows indicate folliculinid ciliates in orifices of adjacent autozooids (also visible in Fig. 7).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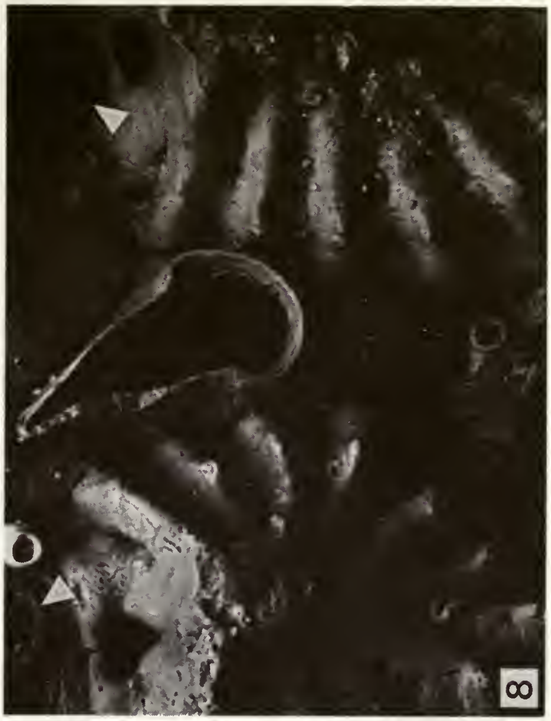
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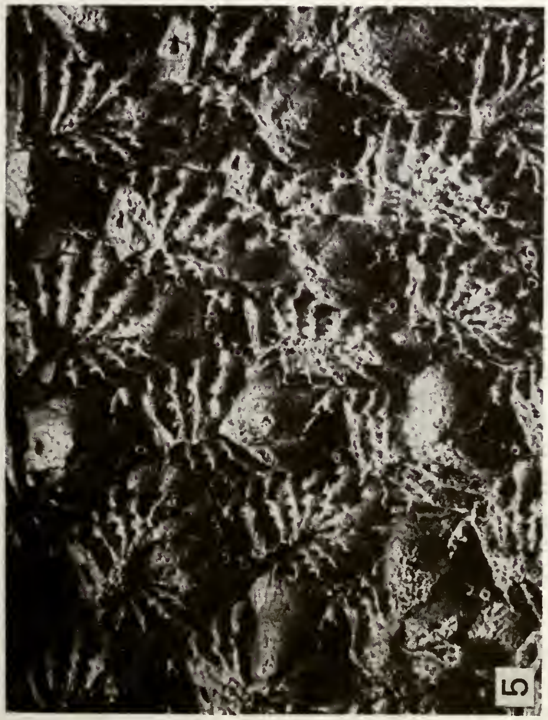
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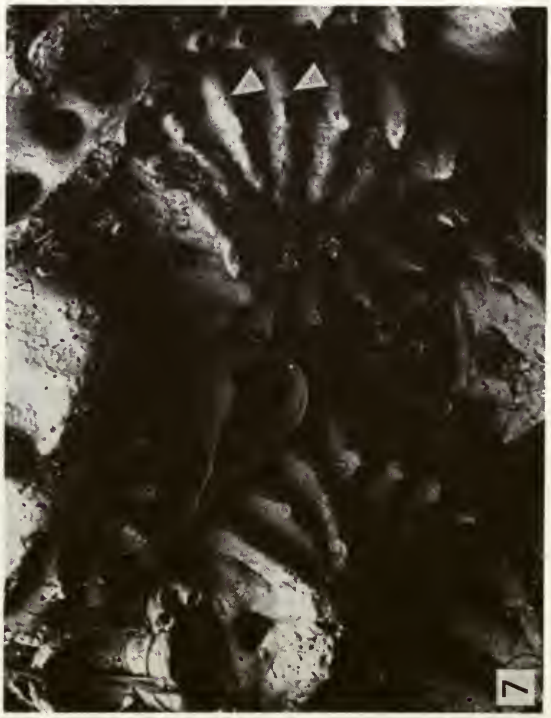
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literature of this supposedly cosmopolitan species are at best equivocal, yet may not be firmly discounted without examination of source material. However it can be stated that, amongst records from Recent seas, Busk (1854: pl. 86 fig. 3 only) and Manzoni (1871) do not refer to *Cribrilaria innominata* as defined by the neotype. Similarly, from the respective descriptions, *Colletosia innominata* subsp. *bifida* d'Hondt, 1970 and *Puellina innominata* var. *vicariata* Waters, 1923 do not in fact belong within *Cribrilaria innominata*. The fossil species *Lepralia mitrata* Seguenza, 1879 and *L. elegantissima* Seguenza, 1879 were both referred to *Cribrilina radiata* form *innominata* by Hincks (1884). Comparison of Seguenza's figures (1879: pl. 15 fig. 8 and pl. 8 fig. 11) with the neotype of *Cribrilaria innominata* clearly indicates the rejection of this synonymy (a conclusion already reached by Neviani (1900) in the case of *L. elegantissima*). The record of *Lepralia innominata* from the Pliocene Coralline Crag of eastern England by Busk (1859) is discounted; the accuracy of the published account was checked in this case by examination of part of the relevant material (BMNH B1697, D6754, D6799 and D6934). Since Manzoni (1869) based his concept of *L. innominata* on Busk's (1859) account and apparently copied Busk's figure, his record from the Italian succession must also be questioned. Indeed, the occurrence of *Cribrilaria innominata*, as defined by the neotype, as a fossil in the European Neogene is regarded as unproven.

The account of *Cribrilaria innominata* given by Hayward & Ryland (1979) agrees in all relevant details with the neotype. BM(NH) 1899.5.1.723, from which at least part of Hayward & Ryland's figure was drawn, is considered to be conspecific with BM(NH) 1847.9.16.32.

The neotype colony shows an example (Fig. 4) of 'total regeneration with oblique polarity axis' *sensu* Jebram (1978: 259 and fig. 4). In this case, the regenerated zooid appears to have been budded from the left distolateral neighbour of its damaged predecessor; it is abnormal in having four rather than five oral spine bases.

The proximally bifid zooids found in the colony (Fig. 3) may represent 'lateral cystid fusions' *sensu* Jebram (1978: 260 and fig. 4). It is probable that three parent zooids (one proximal, two proximolateral) contribute to the development of a bifid zooid. In the observed examples, the orifice shows the same orientation as those of surrounding zooids. An example of a bifid zooid with the orifice oblique (i.e. aligned with one of the proximal branches of the zooid) in an Upper Cretaceous cribrimorph is illustrated by Jebram & Voigt (1977). These authors also list other fossil occurrences of 'heart-shaped' zooids recorded in the literature. In less well developed cases, cribrimorph zooids may simply show extreme proximal widening with partial duplication of the radiating pattern of costae. Waters (1923: 558) recorded specimens referred to *Puellina innominata* 'with the proximal part [of some zooids] spreading out' and cited a similar occurrence in *Castanopora castanea* illustrated by Lang (1922: pl. 5 fig. 2). Proximally bifid zooids and zooids with extreme proximal widening appear to be relatively common in cribrimorphs.

As noted in the redescription above, the most peripheral of the pores between adjacent costae differ in size and morphology from the others. They may prove to be bounded on their outer or more basal margin by gymnocyst rather than intercostal calcification. The term intercostal pores should not, perhaps, be used to include these outer pores. Norman (1903: 96–98), noting that they were distinct, used the term 'papillae-pores' (or 'papillae-holes'), since a series of uncalcified papillae emerge through them (in material in which soft parts are preserved); the most distal and longest pair of these are commonly called setiform papillae. The papillae are found in many species of *Cribrilaria* and *Puellina*, and were cited in the diagnosis of *Puellina* by Levinsen (1909) and Gordon (1984). They were discussed by Smitt (1873), Harmer (1902; 1926), Norman (1903), Levinsen (1909), Waters (1923), Canu & Bassler (1928) and Gordon (1984), and illustrated using SEM by Harmelin (1970: pl. 2 fig. 5; 1984: figs 4, 5, 6 and 7).

Acknowledgements

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References

Anon. 1845. On marine zoology. By Charles William Peach. *Report of the British Association for the Advancement of Science (Transactions of the Sections)* **1844:** 64–65.

Boase, G. C. & Courtney, W. P. 1878. *Bibliotheca Cornubiensis* **2:** i–vii and 418–917. London.

Busk, G. 1854. *Catalogue of marine Polyzoa in the collection of the British Museum. Part 2. Cheilostomata (part.)*, i–viii and 55–120. London.

—— 1859. *A monograph of the fossil Polyzoa of the Crag*, i–xiii and 1–136. London.

—— 1860. Catalogue of the Polyzoa collected by J. Y. Johnson, Esq., at Madeira, in the years 1859 and 1860, with descriptions of the new species. *Quarterly Journal of Microscopical Science* **8:** 280–285.

Canu, F. & Bassler, R. S. 1928. Les bryozoaires du Maroc et de Mauritanie. 2e Mémoire. *Mémoires de la Société des Sciences Naturelles (et Physiques) du Maroc* **18:** 1–85.

—— & —— 1929. Bryozoaires éocènes de la Belgique conservés au Musée Royal d'Histoire Naturelle de Belgique. *Mémoires du Musée Royal d'Histoire Naturelle de Belgique* **39:** 1–68.

Couch, J. 1838. *A Cornish fauna. Part 1. Vertebrate, crustacean and a portion of the radiate animals*, i–vi and 5–84. Truro.

—— 1841. *A Cornish fauna. Part 2. The testaceous mollusks*, i–viii and 1–76. Truro.

Couch, R. Q. 1844. *A Cornish fauna. Part 3. The zoophytes and calcareous corallines*, i–xvii and 1–164. Truro.

Gordon, D. P. 1984. The marine fauna of New Zealand: Bryozoa: Gymnolaemata from the Kermadec Ridge. *New Zealand Oceanographic Institute Memoir* **91,** 1–198.

Gray, J. E. 1848. *List of the specimens of British animals in the collection of the British Museum. Part 1. Centroniae or radiated animals*, i–xiii and 1–173. London.

Harmelin, J. G. 1970. Les *Cribrilaria* (bryozoaires chilostomes) de Méditerranée; systématique et écologie. *Cahiers de Biologie Marine* **11:** 77–98.

—— 1978. Sur quelques cribrimorphes (Bryozoa, Cheilostomata) de l'Atlantique Oriental. *Téthys* **8:** 173–192.

—— 1984. Bryozoaires des peuplements sciaphiles de Méditerranée: révision de *Cribrilina setosa* Waters et description de deux nouvelles espèces de *Cribrilaria* (Bryozoa, Cheilostomata). *Zoologica Scripta* **13:** 81–88.

Harmer, S. F. 1902. On the morphology of the Cheilostomata. *Quarterly Journal of Microscopical Science* **46:** 263–350.

—— 1926. The Polyzoa of the Siboga Expedition. Part 2. Cheilostomata Anasca (with additions to previous reports). *Siboga-Expeditie* **28b:** i–viii and 181–501.

Hayward, P. J. & Ryland, J. S. 1979. British ascophoran bryozoans. *Synopses of the British fauna (New Series)* **14:** 1–312.

Hincks, T. 1880. *A history of the British marine Polyzoa* **1:** i–cxli and 1–601; **2:** 83 pl. London.

—— 1884. Note on Prof. G. Seguenza's list of Tertiary Polyzoa from Reggio (Calabria). *Annals and Magazine of Natural History (Series 5)* **13:** 265–267.

d'Hondt, J. L. 1970. Campagne d'essais du 'Jean Charcot' (3–8 Décembre 1968). 5. Bryozoaires. *Bulletin du Muséum National d'Histoire Naturelle (2e Série)* **42:** 232–256.

Jebram, D. 1978. Preliminary studies on 'abnormities' in bryozoans from the point of view of experimental morphology. *Zoologische Jahrbücher (Anatomie)* **100:** 245–275.

—— **& Voigt, E.** 1977. Monsterzooide und doppelpolypide bei fossilen und rezenten Cheilostomata Anasca (Bryozoa). *Abhandlungen und Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg, N.F.* **20:** 151–173.

Johnston, G. 1847. *A history of the British zoophytes* (2nd edition) **1:** i–xiv and 1–488; **2:** 74 pl. London.

Lagaaij, R. 1952. The Pliocene Bryozoa of the Low Countries. *Mededelingen van de Geologische Stichting (Serie C)* **5:** 1–233.

Lang, W. D. 1922. *Catalogue of the fossil Bryozoa (Polyzoa) in the Department of Geology, British Museum (Natural History). The Cretaceous Bryozoa (Polyzoa). Volume 4. The Cribrimorphs. Part 2*, i–xii and 1–404. London.

Lee, S. (Ed.) 1895. *Dictionary of national biography* **44:** i–vi and 1–447. London.

Levinsen, G. M. R. 1909. *Morphological and systematic studies on the cheilostomatous Bryozoa*, i–vii and 1–431. Copenhagen.

Manzoni, A. 1869. Bryozoi Pliocenici Italiani. *Sitzungsberichte der Akademie der Wissenschaften. Mathematisch-Naturwissenschaftliche Classe. Wien. Abt. 1* **59:** 17–28.

—— 1871. Supplemento alla fauna dei bryozoi Mediterranei. 1a Contribuzione. *Sitzungsberichte der Akademie der Wissenschaften. Mathematisch-Naturwissenschaftliche Classe. Wien. Abt. 1* **63:** 73–82.

Neviani, A. 1900. Briozoi Neogenici delle Calabrie. *Palaeontographia Italica. Memorie di Palaeontologia* **6:** 115–265.

Norman, A. M. 1903. Notes on the natural history of East Finmark. *Annals and Magazine of Natural History (Series 7)* **12:** 87–128.

Peach, C. W. 1882. A catalogue of additions to, and alterations in that of the zoophytes of Cornwall, by the late R. Q. Couch, Esq. *Journal of the Royal Institution of Cornwall* **7:** 149–190.

Seguenza, G. 1879. Le formazioni Terziarie nella Provincia di Reggio (Calabria). *Atti della Reale Accademia dei Lincei (Ser. 3)* **6:** 1–446.

Smitt, F. A. 1873. Floridan Bryozoa. Part 2. *Kungliga Svenska Vetenskapsakademiens Handlingar* **11:** 1–83.

Waters, A. W. 1923. Mediterranean and other Cribrilinidae, together with their relationship to Cretaceous forms. *Annals and Magazine of Natural History (Series 9)* **12:** 545–573.

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A revision of the spider genus *Phyaces* (Araneae: Salticidae)

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Introduction

The genus *Phyaces* Simon 1902, was comprised of two taxa, *P. comosus* Simon, the type species from Sri Lanka and *P. furiosus* Hogg from Sumatra. The latter species lacks the ornate hair tufts of *P. comosus* and is therefore transferred to the genus *Simaetha* Thorell to which it clearly belongs. The species is not redescribed in the present work, but will be dealt with when *Simaetha* is revised.

Interest in *P. comosus* stems from the unusual behaviour, cryptic appearance and bizarre ornamentation of this small salticid spider. They are detritus mimics in life and specimens have been collected from ground litter and litter trapped in the shrub layer of bushes. Several examples were preserved in spirit by the author before their unusual features were fully appreciated and it is unfortunate that only one live female was available for behaviour studies (see Jackson, 1986).

The standard abbreviations and measurements are those used by Wanless (1978*a*), but for the leg spination the system adopted is that used by Platnick and Shadab (1975).

Taxonomy

Genus *Phyaces* Simon

Phyaces Simon, 1902: 399. Type species *Phyaces comosus* Simon, by original designation and monotypy. Simon, 1903: 836, 839, 840, 843. Waterhouse, 1912: 230. Petrunkevitch, 1928: 191. Neave, 1940, III: 736. Roewer, 1954: 1009. Bonnet, 1958: 3647. Prószyński, 1971: 459; 1984: 10. Brignoli, 1983: 628.

DEFINITION. Small spiders adorned with pronounced hair tufts and with legs I enlarged; total length between 2·0–4·0 mm; sexes alike in general habitus. In life, cryptic detritus mimics.

Carapace: of medium height, slightly longer than broad, widest and somewhat bulbous at level of coxae II–III; fovea absent; cuticle sculptured, papillate-falsifoveate with setae, i.e. scattered setose pits with raised papillae-form rims posteriorly; adorned with lateral fringes and dorsal hair tufts. *Eyes:* with moderately pronounced lenses set on low tubercles; laterals with black surrounds; anteriors unequally spaced, medians contiguous, laterals separated from medians by about half their diameter, apices slightly recurved; posterior medians minute, set closer to and well outside optical axis of anterior laterals; posterior laterals about as large as anterior laterals, set just inside lateral margins of carapace when viewed from above; posterior ocular quadrangle clearly wider behind; entire quadrangle about 56% of carapace length. *Clypeus:* low. *Chelicerae:* of medium size, slightly more robust in male; bulbous but with anterior surface somewhat flattened; slightly inclined anteriorly, more or less parallel; fang moderately strong and curved; promargin with two teeth, retromargin with bicuspid tooth. *Maxillae*: moderately long, parallel with outer distal margins more or less rounded. *Labium*: longer than broad, greater than half maxillar length. *Sternum:* scutiform with markedly bulbous central area. *Pedicel:* short. *Abdomen*: set so that anterior part lies over thoracic slope; more or less ovoid and somewhat flattened with pronounced basal hair tuft; spinnerets relatively short, subequal in length, anteriors robust others slender; former position of colulus indicated by scanty group of setae between anterior spinnerets and tracheal spiracle; tracheal system not examined, spiracle an

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indistinct slit near base of anterior spinnerets. *Legs:* first pair enlarged with scanty fringes, others relatively short and moderately robust; claws pectinate, tufts present, scopulae absent; spines few, but vary from normal to robust—strongest on metatarsi I. In males spines present on metatarsi, tibiae and femora of legs I–II and femora of legs III–IV, in females only present on metatarsi and tibiae of legs I–II. *Female palp*: moderately long and hairy.

Epigyne: moderately simple with median triangular pouch not always evident in uncleared specimens; copulatory openings indistinct and associated with large disc-like surrounds (arrowed, Fig. 2D, F); introductory ducts short and relatively broad; spermathecae rounded with large fertilization ducts.

Male palps: simple; femora bowed and laterally flattened; tibiae short with simple unmodified retrolateral apophysis; cymbium with distal scopula; embolus short, slender, arising from distal prolateral margin of tegulum; tegulum rounded with marginal seminal duct; expanded palps not examined.

DIAGNOSIS. The ornate hair tufts readily separate *Phyaces* from other salticid genera.

AFFINITIES. Simon (1903) was correct when he placed *Phyaces* in his subgroup Simaetheae. The general habitus and structure of the genitalia suggesting a relationship with the nominate genus *Simaetha* Thorell and furthermore, as Prószyński (1984) noted, it also shares affinities with *Ligurra* Simon, also in Simaetheae. A casual survey of other genera currently included in the sub group and unidentified specimens in the collections of the British Museum (Natural History), indicates that some genera may be synonymous and that there are possibly many new species to be described. It is also probable that diversity, in respect of habitus may be considerable.

For the present, *Phyaces* can only be treated as valid on the basis of its ornate hair tufts which are evidently autapomorphic for the genus. It could, however, fall into synonymy when the morphological peculiarities of Simaetheae are fully known.

Phyaces comosus Simon

Phyaces comosus Simon, 1902: 399. LECTOTYPE ♂, PARALECTOTYPES 2♀♀, 3♂♂, (here designated) Sri Lanka, (MNHN, Paris). Simon, 1903: 836, 839, 840, 843. Waterhouse, 1912: 230. Petrunkevitch, 1928: 191. Neave, 1940, III: 736. Roewer, 1954: 1009. Bonnet, 1958: 367. Prószyński, 1971: 459; 1984: 110.

MALE from Badulla, in good condition. *Carapace* (Fig. 1B, C): sculptured papillate-falsifoveate with setae (see generic description); orange-brown lightly tinged black in eye region; clothed in scattered black hairs and fine shining greyish setae with long whitish and greyish hairs below lateral eyes and five black hair tufts dorsally, the posterior pair largest, tipped white and mixed with white hairs. *Eyes:* laterals with black surrounds; fringed by shining white and amber hairs. *Clypeus*: clothed in fine long grey hairs below anterior median eyes and long white hairs below anterior laterals; these sweep upwards in space between anterior laterals and anterior medians, to extend as rather scanty tufts above anterior median eyes. *Chelicerae* (Figs. 1E; 2C): rugulose, shiny with scattered finely setose papillae; pale yellow-brown with whitish hair along inner margins; teeth not examined. *Maxillae* (Fig. 1H) pale yellow-brown. *Labium:* pale yellow-brown lightly tinged grey. *Sternum* (Fig. 1G): central region bulbous; yellow-brown with scattered black hairs on margins, suffused black with fine greyish hairs centrally. *Coxae:* first pair large, yellow-brown lightly tinged black; others smaller, mottled black. *Abdomen:* dorsum yellow-brown to pale amber suffused and mottled black with vague chevrons posteriorly and four indistinct apodemal spots; clothed in recumbent fine amber setae and scattered stiff black hairs with an enormous tuft of grey and creamy white hairs anteriorly and inconspicuous scattered white tufts marginally; lateral sides grey with white guanin and black streaks, clothed in whitish and scattered stiff black hairs; venter creamy white mottled black on sides with three longitudinal black bands centrally; clothed in scattered long black hairs with fine whitish ones over paler areas; spinnerets pale yellow lightly tinged black with scattered black and grey-black hairs. *Legs:* first pair enlarged (Fig. 1A), yellow-brown with black mottling on inner and underside of femora, clothed in black and some white hairs forming fringes on femora, patellae and tibiae, also, on

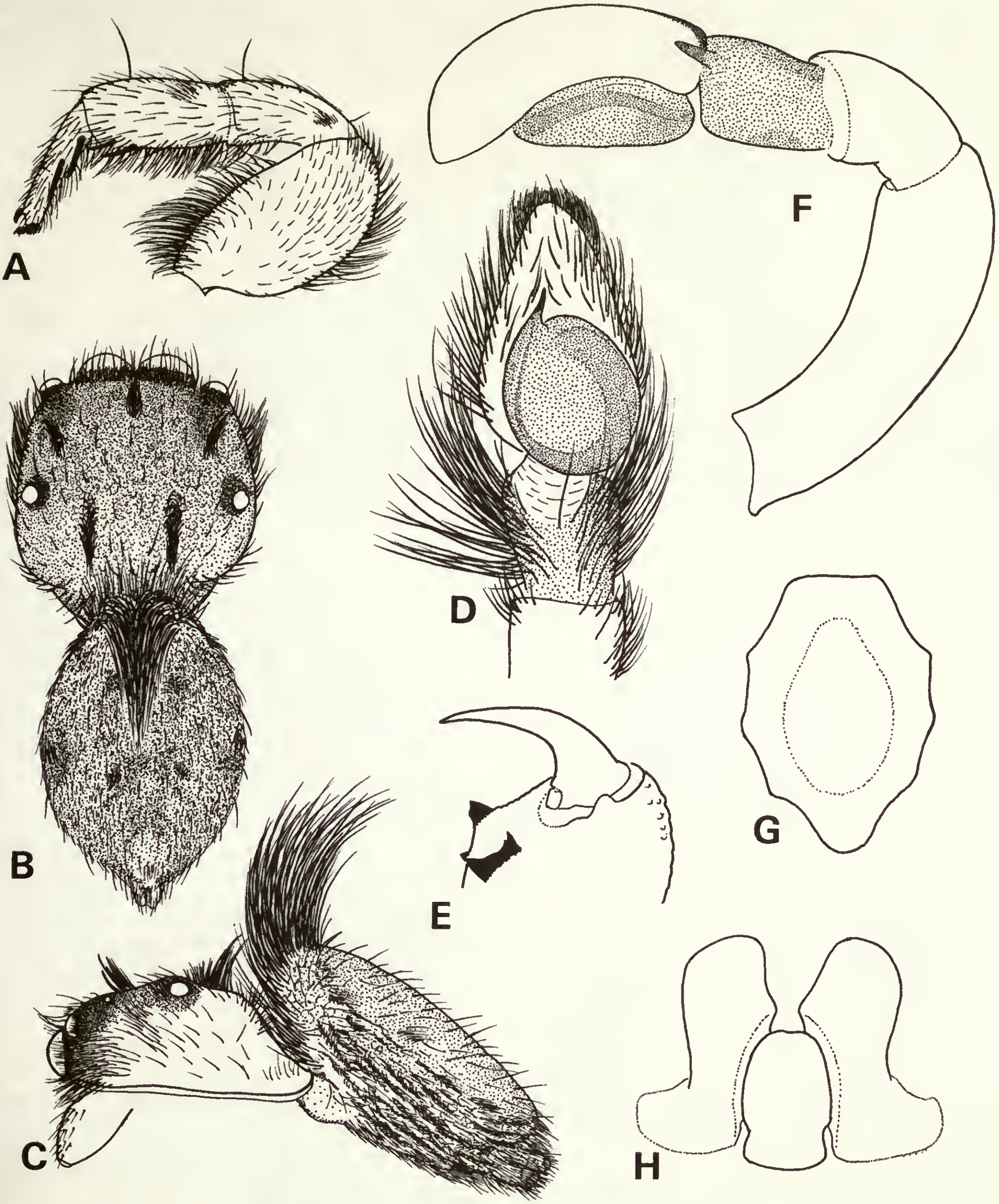

Fig. 1. *Phyaces comosus* Simon, ♂ from Badulla: A, leg I; B, dorsal; C, lateral; D, palp, ventral view; F, palp, retrolateral view. Paralectotype ♂: E, cheliceral teeth; G, sternum; H, maxillae and labium.

tibiae and patellae a thin covering of recumbent iridescent brown hairs; other legs pale yellow-brown grading to greyish white distally with joints and femora mottled black, generally clothed in scattered black and whitish hairs. Spines relatively large and robust on metatarsi I, short and robust on tibiae I, otherwise more or less normal elsewhere; spination of legs I: metatarsi v 2–0–0, p 0–0–1, r 0–0–1; tibiae v 0–0–3; femora d 0–0–3. *Palp* (Fig. 1D, F): yellow-brown clothed in black hairs.

Dimensions (mm): total length 2·92; carapace length ca. 1·52, breadth 1·48, height 0·74; abdomen length 1·96; eyes, anterior row 1·17, median row 1·12, posterior row 1·44; quadrangle length 0·84 (55% of carapace length).

Leg	1	2	3	4	Palp
Femora	1·12	0·76	0·66	0·86	0·56
Patella	0·71	0·44	0·35	0·40	0·24
Tibia	0·68	0·32	0·34	0·42	0·16
Metatarsus	0·32	0·32	0·30	0·36	——
Tarsus	0·32	0·34	0·28	0·30	0·44
Total	3·21	2·20	1·95	2·38	1·40

Ratios: AM : AL : PM : PL :: 8·5 : 4·2 : 0·75 : 4; AL—PM—PL :: 5·5—8; AM : CL :: 8·5 : 1·5.

FEMALE from Dikwella, in fair condition. As male except for the following. *Carapace:* more heavily suffused black in eye region. *Chelicerae* (Fig. 2E) smaller, smoother and with fewer, less conspicuous setose papillae; teeth not examined. *Legs:* spination see generic description; spination of legs I: metatarsi as in male, tibiae v 1–2–1. *Epigyne* (Fig. 2A B, D, F, G): although figured in ventral and posterior aspects, the latter is probably the more usual view point because of the position of the abdomen relative to the carapace.

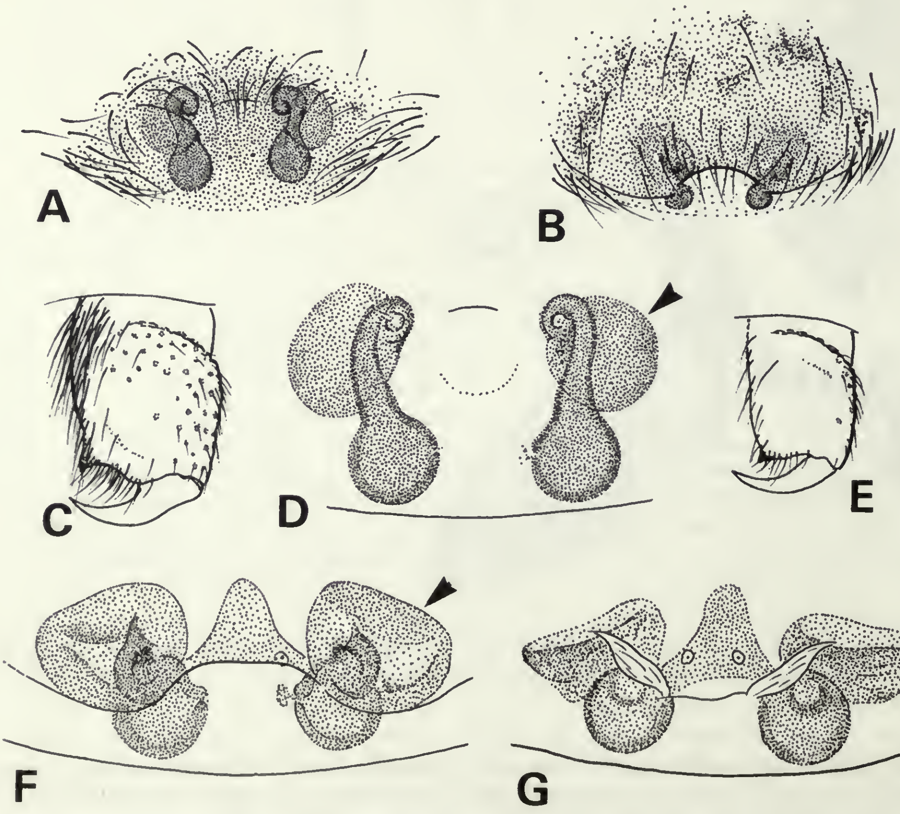

Fig. 2. *Phyaces comosus* Simon, ♀ from Dikwella: A, epigyne, posterior view; B, epigyne, ventral view; D, vulva, posterior view; E, chelicera; F, vulva, ventral view; G, vulva, dorsal view. ♂ paralectotype: C, chelicerae.

Dimensions (mm): total length ca. 2·9 (pedicel stretched); carapace length 1·40, breadth 1·36, height 0·68; abdomen length 1·48; eyes, anterior row 1·14, medium row 1·16, posterior 1·39; quadrangle length 0·8 (57% of carapace length).

Leg	1	2	3	4	Palp
Femur	0·88	0·64	0·56	0·78	0·44
Patella	0·56	0·40	0·28	0·36	0·22
Tibia	0·46	0·32	0·28	0·44	0·24
Metatarsus	0·32	0·32	0·30	0·36	——
Tarsus	0·20	0·24	0·28	0·32	0·32
Total	2·42	1·92	1·70	2·26	1·22

Ratios: AM : AL : PM : PL:: 8 : 4 : 0·8 : 4; AL—PM—PL :: 5·5–7·5; AM : CL :: 8 : ca. 1·5.

VARIATION. Male total length 2·72–2·96 mm, carapace length 1·44–1·52 (four specimens); female total length 2·72–3·16 mm, carapace length 1·28–1·4 mm (four specimens).

In the majority of females there is an orange scutum on the dorsum of the abdomen, which is lacking in males and not evident in the female described above. Also, the abdominal apodemes are sometimes conspicuous, in reality there are four pairs, but the anterior pair are close together, minute and not always evident.

DISTRIBUTION. Sri Lanka.

MATERIAL EXAMINED. **Sri Lanka:** Badulla, Dunhindu Falls, 1♂, ground litter, 20.x.1982, *F. R. Wanless;* Dikwella, nr. Badulla, 1♀, roadside vegetation by paddy field, 20.x.1982, *F. R. Wanless,* (BMNH). Kandy: lectotype ♂, paralectotypes 2♂♂, 3♀♀, *E. Simon,* (MNHN, Paris. 20505); Peradenyia: Royal Botanic Gardens, 1♀, in litter beaten from bamboo, 16.x.1982, *F. R. Wanless;* 1♀, O.P.—Cambridge coll, (UM, Oxford).

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References

Bonnet, P. 1958. *Bibiographia Araneorum* **2** (4): 3027–4230. Imprimerie Douladoure, Toulouse.

Brignoli, P. M. 1983. *A catalogue of the Araneae described between 1940 and 1981.* Manchester University Press in association with the British Arachnological Society.

Jackson, R. R. 1986. The biology of *Phyaces comosus* (Araneae: Salticidae), predatory behaviour, antipredator adaptations and silk utilization. *Bull. Br. Mus. nat. Hist.* (Zool.) **50:** 109–116.

Neave, S. A. 1940. *Nomencl. Zool.* III, M-P: 1065 pp. Zoological Society, London.

Petrunkevitch, A. 1928. Systema Aranearum. *Trans. Conn. Acad. Arts Sci.* **29:** 270 pp.

Platnick, N. I. & Shadab, M. U. 1975. A revision of the spider genus *Gnaphosa* (Araneae: Gnaphosidae) in America. *Bull. Am. Mus. nat. Hist.* **155:** 3–66.

Prószyński, J. 1971. Catalogue of Salticidae (Aranei) specimens kept in major collections of the world. *Annls zool. Warsz* **28** (17): 367–519.

—— 1984. *Diagnostic drawings of less known Salticidae [Araneae]—an atlas.* Wyzsza Szkola Rolniczo—Pedagogiczna w Siedlcach.

Roewer, C. Fr. 1954. *Katalogue der Araneae.* 2, Abt. B: 924–1290. Institut Royal des Sciences Naturelle de Belgique, Bruxelles.

Simon, E. 1902. Descriptions d'arachnides nouveaux de la Famille des Salticidae (Attidae) (Suite) (1). *Annls Soc. ent. Belg* **46:** 363–406.

—— 1903. *Histoire Naturelle des Araignées.* **2** (4): 669–1080. Roret: Libraire Encyclopédique, Paris.

Wanless, F. R. 1978. A revision of the spider genera *Belippo* and *Myrmarachne* (Araneae: Salticidae) in the Ethiopian Region. *Bull. Br. Mus. nat. Hist.* (Zool.) **33** (1): 139 pp.

Waterhouse, C. D. 1912. *Index zoologicus* No II, 324 pp.

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The biology of *Phyaces comosus* (Araneae: Salticidae), predatory behaviour, antipredator adaptations and silk utilization

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Introduction

The salticids are generally considered to be the classic examples of cursorial hunting spiders which, instead of building webs to ensare their prey, use acute vision to stalk, chase, and leap on active insects (Land, 1969*a,b*). However, the evolutionary origins of the salticids and their unique, complex eyes are poorly understood.

Recent studies of *Portia* (Jackson & Blest, 1982; Jackson & Hallas, in press), an unusual salticid genus from Africa, Asia, and Australia, suggest that questions about salticid evolution may not be as intractable as they formerly seemed. Although it moves with apparent ease across open ground and captures prey as a cursorial predator, *Portia** also spins prey-capture webs and invades diverse types of alien webs to prey on the host spiders. Lacking acute vision, typical web-building spiders detect and localize prey and predators by interpreting vibratory disturbances of their webs. Using specialized movements of its legs and palps, *Portia* creates vibrations of the silk that deceive the host spider and assist with predation.

Portia also feeds kleptoparasitically on insects ensnared in alien webs and eats the eggs of the host spider. Eggs are an unusual prey for a salticid, since they are non-motile and salticids are generally envisaged as predators of motile arthropods.

Morphological specializations give *Portia* the appearance of detritus in webs, probably affording it protection from visually hunting predators. Normally, locomotion is slow and 'mechanical', rendering *Portia* difficult to recognize even when moving. When inactive in a web, *Portia* adopts a specialized posture, the cryptic rest posture, with palps retracted to beside the chelicerae and legs retracted to beside and under the body, thus obscuring the outlines of appendages. Away from webs, *P. fimbriata* from Queensland has a specialized means of stalking and catching typical cursorial salticids, a prey which, like *Portia*, has acute vision. This behaviour is unique to this species. When stalking salticids, but not other prey, *P. fimbriata* exaggerates the slow, mechanical nature of its locomotion, retracts its palps as in the cryptic rest posture and ceases to advance when the salticid faces. Apparently, as a result of these behaviours and the cryptic morphology of *P. fimbriata*, salticids fail to recognize *P. fimbriata* as an approaching predator.

Although typical cursorial salticids neither spin webs nor use silk in prey capture, they build silken nests in which they moult, oviposit, mate, and generally stay at night and during other periods of inactivity. A salticid in a nest is probably safe from attacks by many of its predators. However, *P. fimbriata* preys on salticids it locates in nests; it vibrates on the silk, enticing the salticids to come out, or waits patiently until the salticid leaves the nest spontaneously.

Although it is a specialized and complex animal, *Portia* has some morphological characters which are apparently pleisiomorphic (Wanless, 1978, 1984). The occurrence of pleisiomorphic traits in *Portia* raised the intriguing possibility that some of the behaviours of *Portia* are also pleisiomorphic. Recognition of this possibility led to a hypothesis, presented in detail elsewhere (Jackson & Blest, 1982), that the Salticidae evolved from web-building spiders with poorly

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*Except when ambiguity is likely to result *Portia* species will be referred to simply by genus i.e. *Portia* instead of *Portia* spp.

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developed vision and that acute vision evolved originally in a spider similar to *Portia* which became an araneophagic predator proficient at invading diverse types of webs.

It was proposed that some, but not all, of the unusual traits of *Portia* have been inherited from a common ancestor of *Portia* and all other salticids, and that these traits have been lost by most salticids but conserved in members of the genus *Portia*. The specialized manner in which *P. fimbriata* stalks ordinary salticids may have evolved secondarily and uniquely in this species.

Varied types of information are potentially useful for evaluating the Jackson & Blest hypothesis, comparative studies of predatory behaviour and silk utilization in other salticid genera being especially important. *Phyaces comosus* Simon is of special interest because this small salticid, like *Portia*, is a highly cryptic detritus mimic; but *Portia* and *Phyaces* belong to different subfamilies (Wanless, 1986). An opportunity arose to study *P. comosus*, and the results of this study will be reported here.

Materials and Methods

Observations were carried out in the laboratory in Christchurch on a female *P. comosus* collected at Peradeniya, Sri Lanka by F. R. Wanless. Maintenance and testing procedures, terminology, and conventions used in describing behaviour were as in earlier studies (Jackson & Hallas, in press). Various potential nest sites were provided in the form of green leaves, dry dead leaves, stems, pieces of bark, and similar objects spread about in the cage of the *P. comosus*. The spiders and insects with which *P. comosus* was tested and the types of tests for which each species was used are indicated in Table 1 (for additional information, see: Jackson & Hallas, in press).

Cryptic appearance

Because of its unusual morphology and a specialized posture, *P. comosus* was exceedingly well concealed from human observers while standing on dead brown leaves; and on green leaves it was

Table 1. Spiders and insects (*Drosophila* only) used as potential prey or as sources of eggs, webs, and nests in tests with *Phyaces comosus*, listed alphabetically by species. A: adult spider or insect; body lengths: salticids (10–14 mm), insect (*c.* 2 mm). CF: *P. comosus* put into cage with spider or insect; cage free of nests and webs. CP: spider or insect put in cage with *P. comosus* in its nest. CS: spins cribellate sticky web. Cu: non-salticid cursorial spider. ES: ecribellate sticky web. J: juvenile spider; body length: *c.* 2 mm. NE: eggs in vacant nest. NO: nest occupied by host spider, but no eggs present. NS: non-sticky web. NSE: nest with eggs, occupied by host spider. NV: vacant nest with no eggs. Or: Oregon strain (functional wings). S: typical cursorial salticid. SS: social species; builds communal web. Vg: vestigial winged strain (flightless). WB: web-building spider. WE: eggs in vacant web. WO: web occupied by host spider. WI: insect on vacant web of *S. mimosarum.* WV: vacant web with no eggs.

Species	Family	Description	Types of Tests
Achaearanea sp. 1	Theridiidae	A,WB,ES	WE,WV
Araneus pustulosa (Walckenaer)	Araneidae	A,WB,ES	WV
Badumna longinquus (L. Koch)	Amaurobiidae	J,WB,CS	WO
Bavia aericeps (Simon)	Salticidae	A,S	NE, NSE, NV
Cambridgea antipodiana (White)	Stiphidiidae	A,WB,NS	WV
Clubiona cambridgei (L. Koch)	Clubionidae	A,Cu	NSE
Dolomedes minor (L. Koch)	Pisauridae	J,Cu	CF,CP
Drosophila melanogaster Or (Meigen)	Drosophiliidae	A	CF,CP,WI
Drosophila melanogaster Vg (Meigen)	Drosophiliidae	A	CF,CP,WI
Mopsus mormon (Karsch)	Salticidae	A,S	NSE
Stegodyphus mimosarum (Pavesi)	Eresidae	A,WB,CS,SS	WV
Trite auricoma (Urguhart)	Salticidae	J,S	CF,CP,NO

conspicuous but unanimal-like in appearance, resembling instead a speck of dust or a minute bit of detritus.

P. comosus always stood with its legs and palps held very close to the body. Often tarsi II and III were held slightly under the body. Tarsi I tended to be just in front of the chelicerae. The palps were held very close to the front of the chelicerae, sometimes pressing against them. The femur of each palp angled up, with the remainder of the palp angling straight down. When mildly disturbed, *P. comosus* often pulled its appendages in even closer to the body and remained inactive.

Locomotion

While walking, *P. comosus* remained highly cryptic. Its legs moved in short, slow, barely noticeable steps and remained close to the body. Sometimes legs and palps were held closer to the body while stepping than while standing. While stepping, the spider's body rocked forward and backward in a characteristic 'bouncing' fashion (Fig. 1). Usually, the spider rocked forward-backward-forward, making a net advance of *c.* $\frac{1}{2}$ a body length, and a pause of 1–10 s occurred before the next bout started.

Although it occasionally leapt as far as 4 body lengths across barriers such as spaces of a few millimetres between stems, *P. comosus* usually made detours by, for example, returning to the base of the stem then walking across to the base of the other stem.

No waving of legs occurred either while stepping or during pauses between bouts of stepping; but an inconspicuous form of palp waving sometimes occurred. As the waving palps moved up and down, in matching phase, a fraction of a millimetre, they remained close to the front of the chelicerae. When chased vigourously with a brush, *P. comosus* stopped rocking and stepped more rapidly than during normal locomotion. Nevertheless, its movements continued to be much slower then the normal locomotion of typical salticids.

If forced on to a web, *P. comosus* always left immediately. Locomotion across non-sticky webs appeared laboured, and *P. comosus* adhered to cribellate and ecribellate sticky webs, eventually freeing itself after biting at threads and pulling forcefully with its legs.

Nests

The spider never built a nest unless it had access to two dead leaves, with their surfaces only a few millimetres apart, between which to spin. A thick layer of silk was spun against the surface of each leaf. On each of two opposing sides, a more sparsely woven sheet connected the two thick sheets and held the leaves together. The resulting nest had the shape of a flattened tube, *c.* 10 mm long, 7 mm wide and 2 mm deep and open at both ends. Two to six rivets (bands of silk *c.* 2 mm long, 0·5–1·0 mm wide, strung between the leaves) were widely spaced about the nest. The two leaves were very tightly bound by the silk of the rivets and the sides of the nest.

Predatory behaviour

Although *Drosophila* were pursued only occasionally (vestigial: 9 or 16 tests; Oregon: 3 of 12 tests), *P. comosus* readily pursued salticids (6 of 9 tests). However, essentially the same predatory behaviours occurred with both prey-types. *Dolomedes* were ignored by the *P. comosus* (8 tests).

P. comosus usually began to approach its prey, in its usual rocking gait, from 25–35 mm away; and its rocking movements became progressively slower and of lower amplitude as it got closer, especially as it came to within 5–10 mm. There was no tendency for *P. comosus* to behave differently depending on prey orientation. Generally, *P. comosus* did not wave its palps while pursuing its prey.

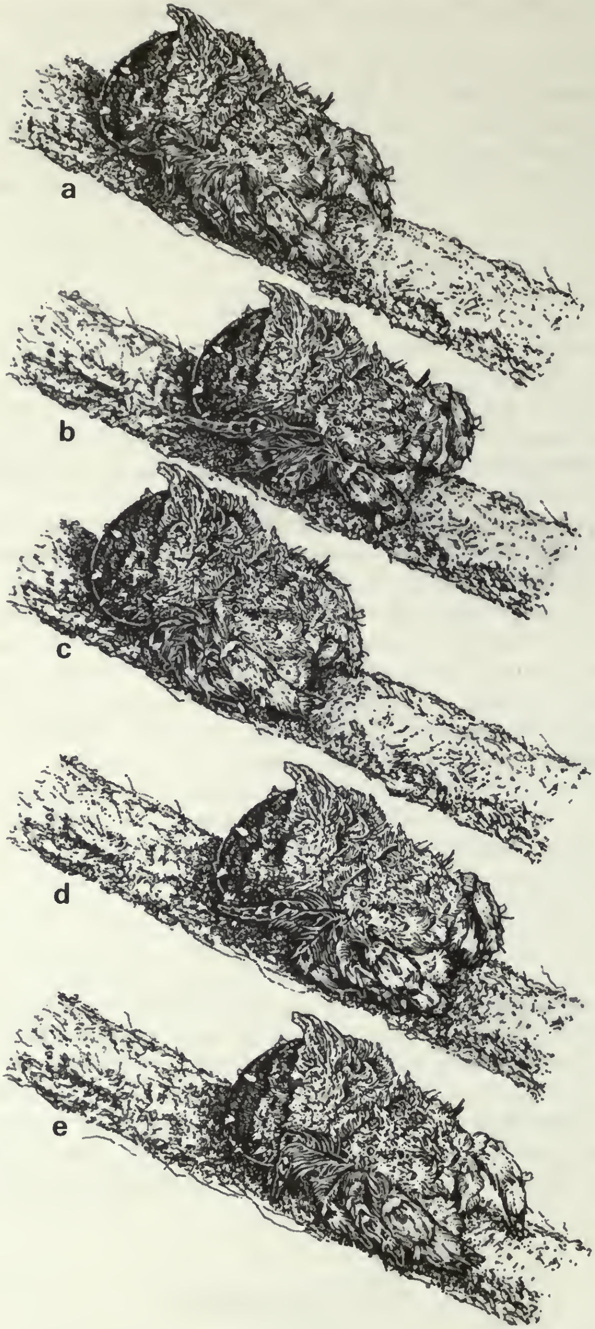

Fig. 1. *Phyaces comosus* Simon. Walking pattern on a stem: (a) Initial position as begins to rock body forward. (b) Maximum forward position before begins to rock backward. (c) Maximum rearward position before starting to move forward again. This position is slightly forward of the initial position. (d) Maximum forward position at the end of the second rock forward. This position is slightly beyond the maximum forward position during the first motion. Barely perceptible shifting of legs across the substrate occurred as the spider rocked forward and backward. (e) Legs are shifted forward as the spider prepares for the next bout of rocking.

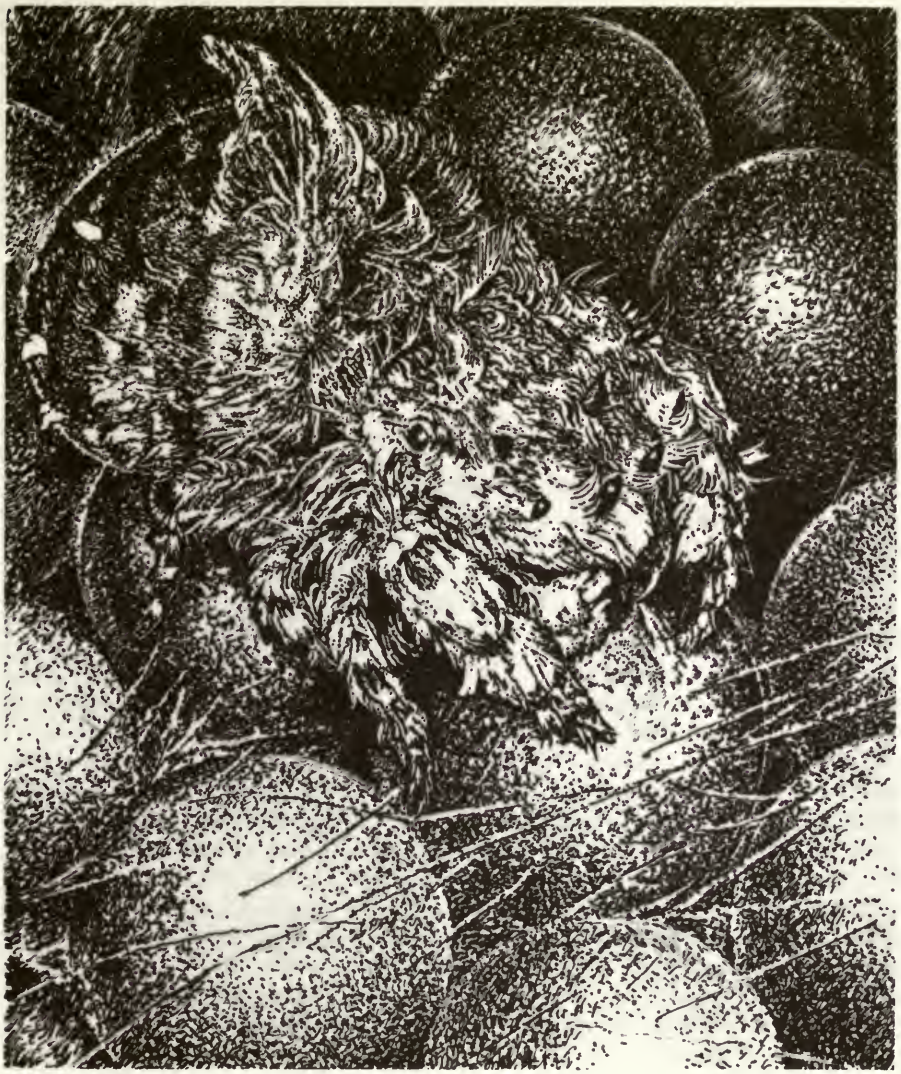

Fig. 2. *Phyaces comosus* Simon eating an egg of a much larger salticid (*Bavia aericeps* Koch). Its fangs are piercing the chorion of the egg. The eggs are almost equal in size to the *P. comosus*.

When $\frac{1}{2}$–1 body length away, *P. comosus* stood inactive for 1–10 s, occasionally longer, then suddenly lunged forward and grasped its prey. There were no evident preliminaries to lunging (legs were not lifted, etc.). Prey was grasped with chelicerae alone. *P. comosus* was observed to capture a *D. melanogaster* only twice (vestigial winged in both cases), but all pursued salticids were captured.

P. comosus never entered webs voluntarily and never attacked juvenile web spiders (24 tests), eggs (4 tests), or ensnared *Drosophila* (10 tests). If it accidently contacted the edge of a web, it moved away immediately (2 tests).

P. comosus always responded distinctively to the nests of cursorial spiders, whether occupied (8) or vacant (3). *P. comosus* intermittently chewed (opened and closed its chelicerae against the silk) or tugged (lifted its cephalothorax once or twice while holding onto the silk with its chelicerae) and gradually made a hole into which it placed legs I. The hole was slowly enlarged as *P. comosus* burrowed its way into the interior of the nest (time elapsing from initial contact with the nest: 0·2–3 h). The 4 small juvenile salticids tested left their nests as *P. comosus* entered, but there were no evident responses by the 3 adult salticids and the one adult clubionid tested. If no eggs were present in the nest, the *P. comosus* eventually left (maximum latency: 4 h); but *P. comosus* fed if eggs were present. Additional layers of silk separated eggs from the inner chamber of the nest; and to feed, *P. comosus* burrowed through this layer then walked on to and pierced an egg with its fangs. After feeding, *P. comosus* remained in the nest near or on the eggs for up to 6 days, sometimes feeding on one or two additional eggs. Host spiders were 8–14 mm in body length, and their eggs were almost as large as the *P. comosus* (Fig. 2).

Discussion

Crypsis

As a result of its specialized locomotory behaviour and its unusual morphology and posture, *P. comosus* is a decidedly cryptic spider, closely resembling small particles of detritus that are common on the ground and on leaves in the understory of the Sri Lankan rain-forest. By choosing dead, dried leaves for nest sites, *P. comosus* is able to move out on to a background against which it is maximally concealed when it ventures forth from its nest.

Locomotion

Functionally, the locomotory behaviour of *P. comosus* is comparable to that of *Portia* and many other highly cryptic, leaf-mimicking and stick-mimicking arthropods (Robinson, 1969). Locomotion occurs in a manner that minimizes the extent to which the animal's specialised camouflage is sacrificed, but there are major differences in the motor patterns employed. The legs and palps of *Portia* move in a unique 'choppy' fashion; *P. comosus* steps in a completely different forward-and-backward rocking gait.

The normal locomotion of most salticids is rapid and agile, and leaps across barriers are made readily. *Portia* and especially *P. comosus* are reluctant to leap. *Portia*, however, unlike *P. comosus*, is quite capable of moving agilely and rapidly if stressed. Although it walks faster and abandons its bouncy gait when chased vigorously, *P. comosus* continues to move atypically slowly for a salticid. *P. comosus*, like African chameleons (Guppy & Davison, 1982) seems to be incapable of running. It is difficult to understand the evolution of an inability to retreat rapidly from predators. Perhaps crypsis is so extreme in *P. comosus* that rapid escape is rarely required. It would be interesting to look for structural or physiological constraints which might hinder rapid movements by *P. comosus*.

Predatory behaviour

The predatory behaviour of *P. comosus* consists primarily of using its normal locomotory gait to approach the prey, slowing down when close, and making a sudden lunge from close range. The manner in which *P. comosus* stalks prey, like its specialized gait during normal locomotion is consistent with crypsis and most probably maintains its concealment from visually hunting predators; but it is inefficient as a means of capturing motile insects (*Drosophila*). It is efficient, however, against a type of prey which is itself a visually hunting predator, namely other salticids. Both *P. comosus* and *Portia fimbriata* have a pronounced tendency to pursue salticids and a relatively weak tendency to pursue insects, suggesting that salticids are a primary prey of *P. comosus*. Crypsis most probably evolved initially as an antipredatory rather than a predatory adaptation, antipredatory crypsis possibly preadapting both species as specialized predators on salticids. Compared to *P. comosus*, the behaviour used by *P. fimbriata* when pursuing a salticid as prey is more discrete from normal locomotion and from predatory behaviour used against other types of prey. With its shorter legs and more hirsute body, *P. comosus* may be a more thoroughly cryptic spider than *P. fimbriata*. Thus it might have less to gain by 'refinements' of the types used by *P. fimbriata*. Also the normally larger salticid prey of the larger (*c.* 10 mm) *P. fimbriata* may tend to have vision of greater acuity than the minute salticids with minute eyes preyed on by the small *P. comosus* in the dimly lit understory of the forest (Blest, in press).

Considering the differences in the behaviour of *P. fimbriata* and *P. comosus* when pursuing salticids and the disparate taxonomic placements of these two species, specialized stalking of salticids most likely evolved convergently. Cursorial salticids are extraordinarily abundant in the Queensland habitat of *P. fimbriata*, and this may have been a major factor favouring the evolution of specialized predation on salticids by this species. Salticids did not seem comparatively abundant in the habitat of *P. comosus*, although small salticids easily could have been overlooked. *P. comosus* and *P. fimbriata* have another behaviour in common, which is shared by all studied *Portia*: feeding on the eggs of other spiders. Differences in the oophagic behaviours of *Portia* and *P. comosus* are evidently related to differences in the sizes of these spiders. *Portia* either bites into the egg sac and eats out its contents as a single entity, or it opens up egg sacs, rakes out the eggs, and feeds on them one at a time. The much smaller *P. comosus* bores into egg sacs, stands on the eggs, and eats them one at a time.

Salticids and clubionids will attack if they detect intruders at the nest (Eberhard, 1974; Jackson, 1976; Pollard, 1983). However, with its small size, stealthy movements, and cryptic morphology, *P. comosus* avoids attracting the attention of and eliciting attacks from the maternal spider. As a distinctly araneophagic spider, *Portia* is in frequent proximity of spider egg sacs, and this was probably an important factor in the evolution of oophagy in this genus. Oophagy probably evolved independently in *P. comosus*, crypsis and small size being important preadaptations. Each egg of a large spider is almost as large as the *P. comosus*, and the egg mass in a single egg sac is a veritable bonanza. The adaptive advantage of oophagic behaviours for *P. comosus* are readily apparent.

Evolutionary implications

To evaluate the proposal that the unique combination of behaviours that occurs in *Portia* is partially a reflection of salticid ancestry, it will be important to ascertain the distribution of these behaviours within the Salticidae. Detritus mimicry, oophagy and specialized predation on salticids are three unusual characteristics that probably evolved independently in *P. comosus* and *Portia*. However, web-building and web-invading with the use of aggressive mimicry, which were proposed as characteristics of salticid ancestors, do not occur in *P. comosus*, suggesting that these are evolutionarily conservative characters, as implied by the Jackson & Blest hypothesis.

A more exhaustive study of *Phyaces* would be interesting; but the prospects for this are dim because of the remoteness, for most arachnologists, of the natural habitats of these spiders and the considerable difficulty of locating *Phyaces* in the field, which is at least partly due to its mimicry of detritus and its small size.

Acknowledgements

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References

Blest, A. D. In press. Retinal mosaics of the principal eyes of jumping spiders (Salticidae) in some Neotropical habitats: optical trade-offs between size and habitat illuminances. *J. Comp. Physiol.*

Eberhard, W. G. 1974. Maternal behaviour in a South American *Lyssomanes*. *Bull. Br. Arachnol. Soc.* **3:** 51.

Guppy, M. & Davison, W. 1982. The hare and the tortoise: metabolic strategies in cardiac and skeletal muscles of the skink and the chameleon. *J. exp. Zool.* **220:** 289–295.

Jackson, R. R. 1976. Predation as a selection factor in the mating strategy of the jumping spider *Phidippus johnsoni* (Salticidae, Araneae). *Psyche* **83:** 243–255.

Jackson, R. R. & Blest, A. D. 1982. The biology of *Portia fimbriata*, a web-building jumping spider (Araneae, Salticidae) from Queensland: utilization of webs and predatory versatility. *J. Zool. (Lond.)* **196:** 255–293.

Jackson, R. R. & Hallas, S. E. A. In press. Comparative biology of *Portia africana, P. albimana, P. fimbriata, P. labiata,* and *P. schultzi*, araneophagic, web-building jumping spiders (Araneae, Salticidae): utilization of webs, predatory versatility and intraspecific interactions. *N.Z. J. Zool.*

Land, M. F. 1969*a*. Structure of the retinae of the principal eyes of jumping spiders (Salticidae: Dendryphantinae) in relation to visual optics. *J. exp. Biol.* **51:** 443–470.

Land, M. F. 1969*b*. Movements of the retinae of jumping spiders (Salticidae: Dendryphantinae) in response to visual stimulti. *J. exp. Biol.* **51:** 471–493.

Pollard, S. D. 1983. Egg guarding by *Clubiona cambridgei* (Araneae: Clubionidae) against conspecific predators. *J. Arachnol.* **11:** 323–326.

Robinson, M. H. 1969. Defenses against visually hunting predators. *In:* Dobzhansky, T., Hecht, M. K. & Steere, W.C. (Eds.) *Evolutionary Biology* **3:** 225–259. New York: Meredith.

Wanless, F. R. 1978. A revision of the spider genus *Portia* (Araneae: Salticidae). *Bull. Br. Mus. nat. Hist.* (Zool.) **34:** 83–124.

Wanless, F. R. 1984. A review of the spider subfamily Spartaeine nom. n. (Araneae: Salticidae) with descriptions of six new genera. *Bull. Br. Mus. nat. Hist.* (Zool.) **46:** 135–205.

Wanless, F. R. 1986. A revision of the spider genus *Phyaces* (Araneae: Salticidae). *Bull. Br. Mus. nat. Hist.* (Zool.) **50:** 103–108.

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Capitella caribaeorum sp. nov., a new capitellid polychaete from the Caribbean

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Introduction

The capitellid polychaete described below has been found intertidally amongst decaying mangrove leaves in southern Florida, Cuba and St Lucia. It forms a network of galleries, lined with mucus and faeces (Fig. 1a), through the surface layers of organic debris accumulated around mangrove roots. The worm has been cultured in agar through many generations (George, 1975) and its behaviour and life history have been elucidated from observations made both in the field and in the laboratory (George, 1984). Initially it was thought that the worm could be assigned to *Capitella giardi* (Mesnil, 1897), but subsequent study has shown that sufficient morphological, behavioural and physiological differences exist to warrant erection of a new species.

The description given below is based on adults collected from the natural habitat and supplemented by observations made on specimens from laboratory culture. No morphological differences were detected between worms from the wild populations and those from a culture that had been maintained in the laboratory for five years.

Specimens collected in the field were fixed in 10% neutralized commercial formalin in seawater for 48 hours before storage in 80% ethyl alcohol. Specimens derived from the cultures were either relaxed by slow addition of alcohol to seawater containing the worms prior to formalin fixation or were anaesthetized by slow addition of glutaraldehyde before fixation in 2·5% glutaraldehyde in 0·1 M phosphate buffer (pH 7·2) with 0·5 M sucrose. Material was dehydrated through the alcohols prior to examination by optical or scanning electron microscopy (SEM). Specimens to be examined by SEM (Hitachi S-800) were either air-dried using diethyl ether or acetone, or dried in an Edwards-Pearse tissue dryer—EPD3, using acetone and liquid CO_2, before coating with gold/palladium in a Polaron sputter coating unit.

Description of new species

Capitella caribaeorum sp. nov.

TYPES. The holotype is a fully grown specimen containing oocytes. The paratypes include specimens that have not reached physical maturity. The holotype (registration no. BM(NH) ZB. 1985. 191) and paratypes (registration nos. BM(NH) ZB. 1985. 192–196) are deposited in the collections of the British Museum (Natural History). Further paratypes have been deposited in the collections of the National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A. and in the Australian Museum, Sydney.

TYPE LOCALITY. Southern Florida red mangrove (*Rhizophora mangle* Linnaeus) swamp, Matheson Hammock, Miami, Florida, U.S.A.

MORPHOLOGY. The species is small with fully grown individuals measuring up to 20 mm in length and 0·7 mm in width across the mid-thorax. The body is divided into a relatively muscular

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thorax followed by a longer thinner abdomen which, unlike that of other capitellids such as *Mediomastus*, remains uncoiled when the worm is handled and when preserved (Fig. 1a). Living worms are light brown in colour and more or less transparent, at least in the abdominal region. Gravid worms show a distinctive banding pattern when stained with methyl green in alcohol (Banse, 1970). Segments 5–8 are stained all over, segment 4 shows only slight colouration and segment 9 does not take up the stain at all. As the stain is gradually washed out the sides of segments 7 and 8 retain the green colour longer than other parts of the worm. This staining pattern is less obvious in non-gravid individuals.

The prostomium is roughly conical, as broad at the base as it is long, and without a palpode. Its dorsal surface is flattened or slightly concave and there is a marked longitudinal ventral cleft (Fig. 1b). There are no obvious nuchal organs. Eyes are not visible in the adult, but a pair of eyes can be seen in a dorso-lateral position to the rear of the prostomium in larvae and recently metamorphosed juveniles.

The peristomium is about the same length as the prostomium but broader, with a large mouth situated ventrally (Fig. 1b). In living worms the demarcation between prostomium and peristomium is clearly visible, but in preserved material the distinction may be less obvious. There is a large eversible proboscis without obvious papillation.

There are nine thoracic chaetigers followed by an abdominal region with up to 40 segments. Thoracic segments are about three times as wide as long anteriorly, narrowing to twice as wide as long posteriorly. The surface is distinctly reticulated. There are no parapodial lobes, but there are widely separated notopodial and neuropodial chaetal bundles positioned half way to two-thirds back on each segment.

Both capillary chaetae and hooded hooks are present in the thorax. In fully grown worms chaetigers 1–6 bear capillaries exclusively in both notopodia and neuropodia. Chaetiger 7 typically has capillaries in the notopodia and hooded hooks in the neuropodia (Figs 1b; 2a). In chaetigers 8 and 9 there are no notopodial capillaries or hooded hooks; instead these segments bear stout genital hooks mid-dorsally and hooded hooks in the neuropodia (Figs 1c; 2a). This arrangement gives a thoracic chaetal formula of 1–6c $7^{\mathrm{C}}_{\mathrm{H}}$ $8\text{–}9^{\mathrm{G}}_{\mathrm{H}}$. However, this formula varies with age and size (see CHAETAL VARIATION).

The number of chaetae in any one bundle is small. There are usually 3 capillaries or 3 hooded hooks per bundle in the thorax (range 2–4) (Fig. 1b). Genital hooks develop in all individuals: usually 1–2 pairs point posteriorly on chaetiger 8 (Fig. 1c) and 1 pair points anteriorly on chaetiger 9. Older individuals have 3 pairs on chaetiger 8 and 2 pairs on chaetiger 9 but the second or third pairs are often very small (presumably replacements) and may be overlooked. The genital hooks on chaetiger 8 slightly overlap those on chaetiger 9 (Fig. 1c). The genital hooks surround a glandular pit similar to that found in male *Capitella capitata*.

The capillary chaetae are prominent. Using optical microscopy each capillary looks winged and has a distinct shoulder slightly above the exit point from the body. Using scanning electron microscopy it can be seen that the winged appearance is caused by the arrangement of the cylinders of which the chaeta is comprised (Figs 1d, e).

The hooded hooks are much shorter than the capillaries and only protrude a short way from the body (Fig. 3a). They each have a shoulder like that of the capillary chaeta, but in this case the shaft terminates in a pointed hook surrounded by a hood which is transparent in transmitted

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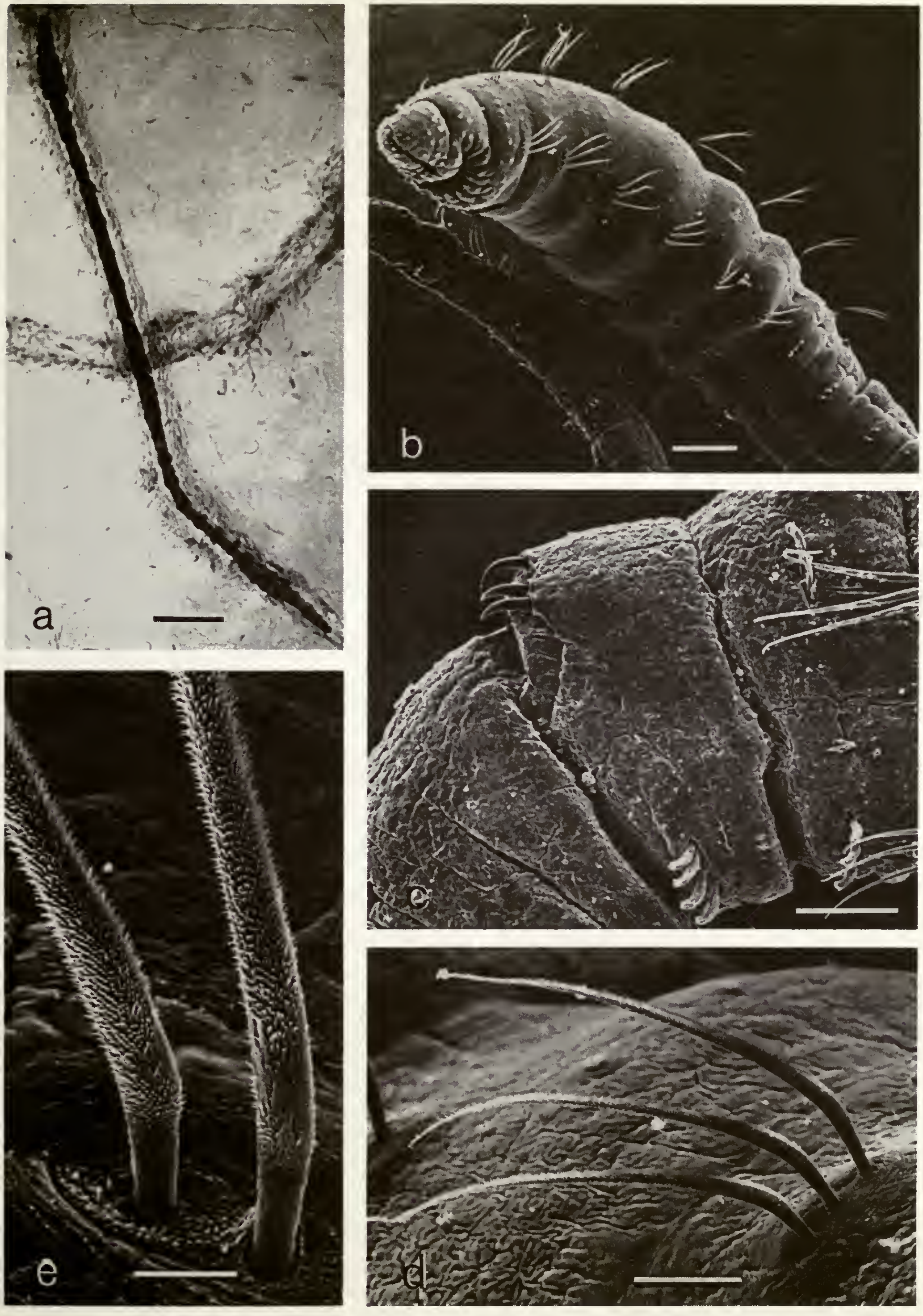
Fig. 1. a: A living adult of *Capitella caribaeorum* showing the general body proportions. The worm is in its burrow which is lined with mucus and faecal pellets (scale bar = 1·5 mm). b: Ventro-lateral view of the head and thorax of an adult. A few segments of the posterior part of the abdomen are also visible, lying alongside the anterior end (scale bar = 130 µm). c: A lateral view of part of the thorax of a sexually mature worm showing the dorsally situated, backwardly pointing, genital hooks of chaetiger 8. (The forward pointing genital hooks of chaetiger 9 are obscured from view) (scale bar = 60 µm). d: Three capillary chaetae of a thoracic notopodium (scale bar = 25 µm). e: A lateral view of two capillary chaetae showing details of their construction (scale bar = 7 µm). (Fig. 1a, transmitted light photograph; Figs. 1b–e, scanning electron micrographs).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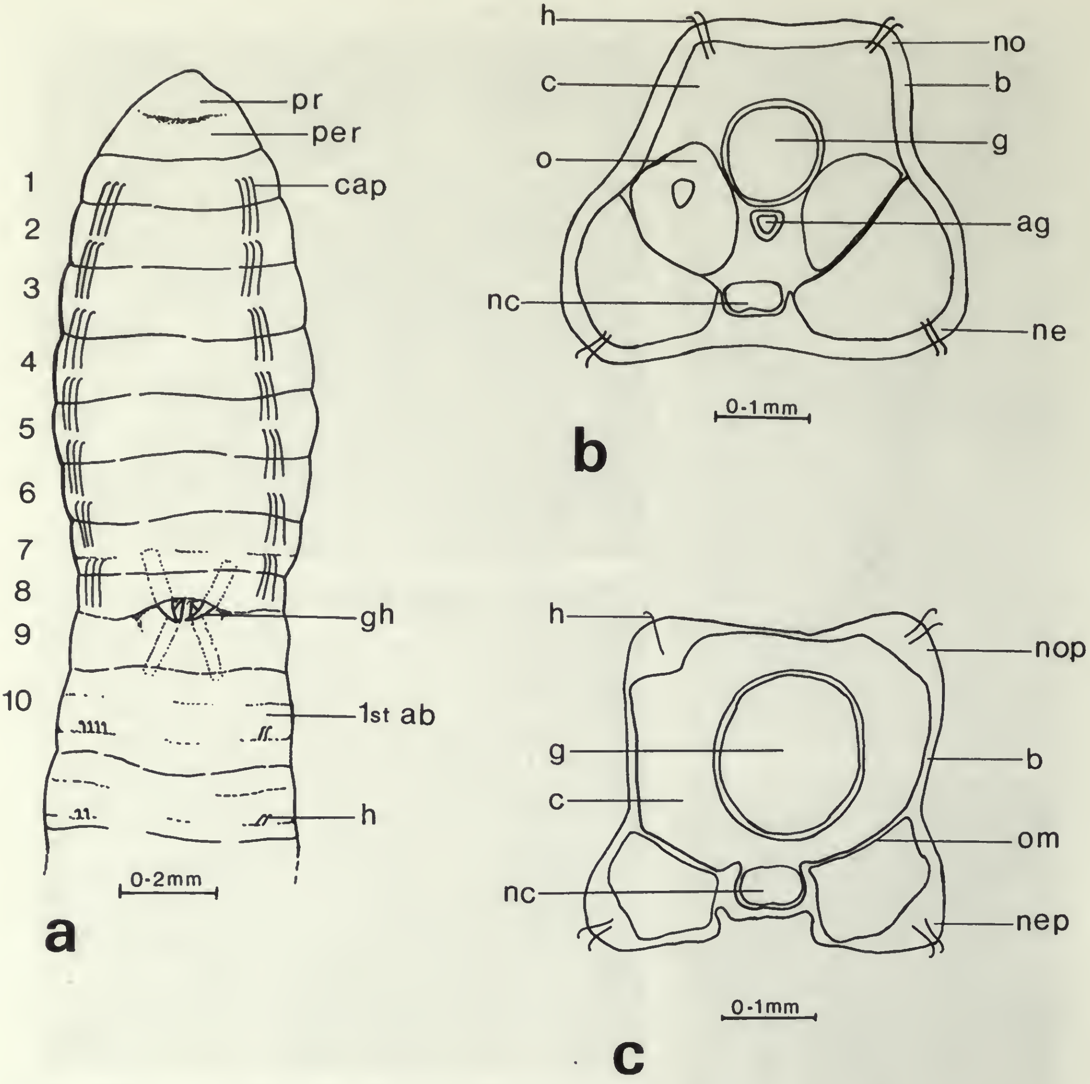
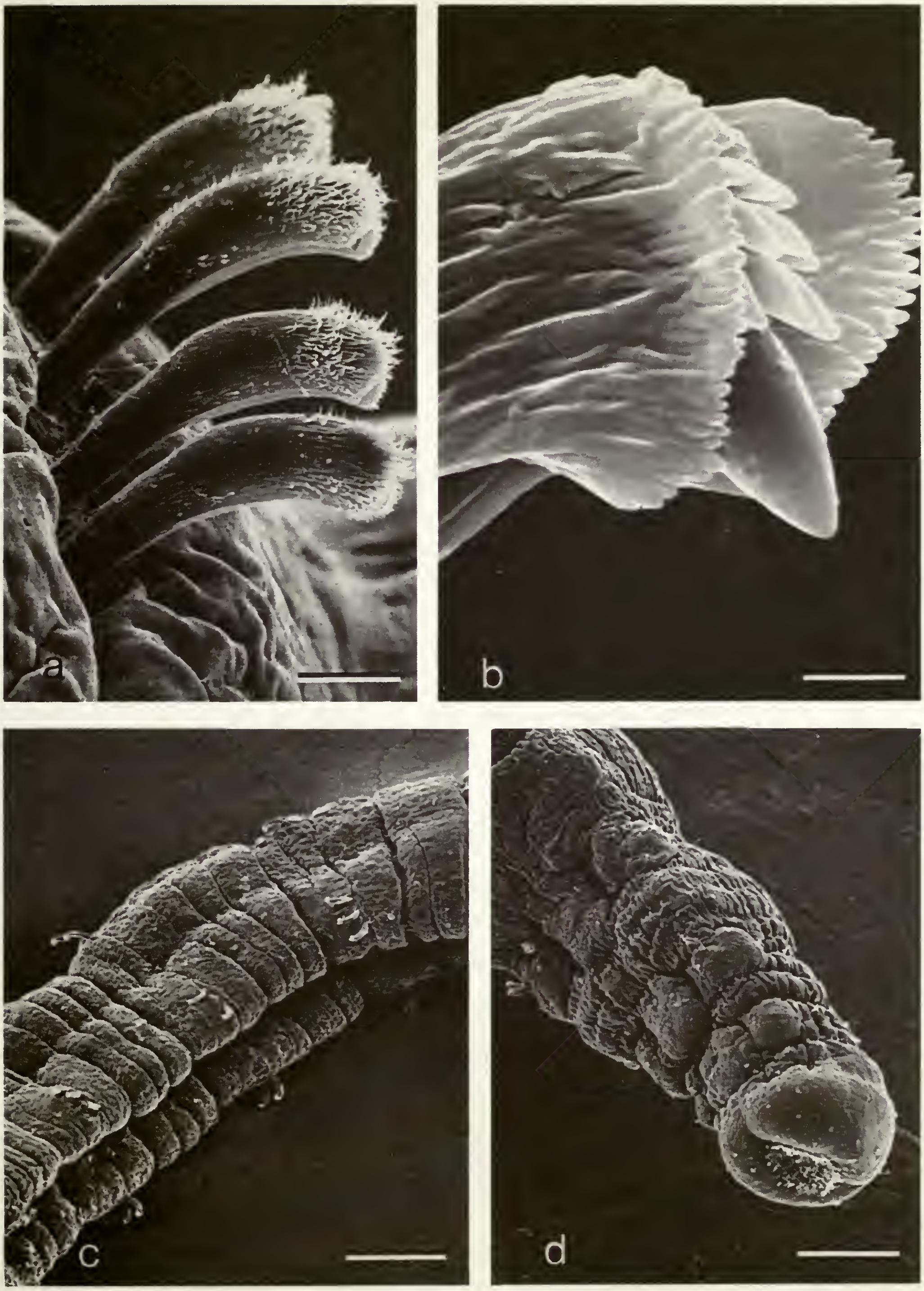


Fig. 2. a: Dorsal view of anterior end showing arrangement of thoracic chaetae. b: TS through an anterior abdominal segment. c: TS through a posterior abdominal segment. ag—accessory gut; b—body wall; cap—capillary chaeta; c—coelom; g—gut; gh—genital hook; h—hooded hook; nc—nerve cord; ne—neuropodium; nep—neuropodial pad; no—notopodium; nop—notopodial pad; o—oocyte; om—oblique muscle; per—peristomium; pr—prostomium; 1st ab—first abdominal segment. Numbers refer to chaetiger number.

Fig. 3. a: A bundle of four hooded hooks protruding from the body wall (scale bar = 7 µm). b: Detail of the head of a hooded chaeta showing the main fang-like tooth overlain by smaller teeth (scale bar = 1 µm). c: A view of the abdomen showing the rectangular box-shaped segments with widely spaced bundles of chaetae (scale bar = 85 µm). d: The posterior end of the body showing the glandular pygidium and the area of segment proliferation immediately in front of it (scale bar = 65 µm). (Figs. 3a–d, scanning electron micrographs).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light. Using scanning electron microscropy it can be seen that the hood consists of several layers of small diameter cylinders which form the outer layer of the chaeta below the shoulder (Fig. 3a). The hook itself is comprised of a large fang-like tooth overlain by several rows of smaller teeth (Fig. 3b). The fang and teeth are the ends of the larger cylinders forming the core of the chaeta. The number and arrangement of the teeth as viewed using light microscopy are not reliable taxonomic characters.

As in most capitellids the junction of thorax and abdomen is not always clearly defined externally, although the groove between segments 9 and 10 is usually more obvious than grooves between preceding thoracic segments. Abdominal segments are thin-walled and transparent when compared with those of the thorax in both living and preserved animals (Fig. 1a). The anterior abdominal segments are about the same length as posterior thoracic ones and are at least as long as wide, but the length:width ratio increases posteriorly until segments become two to three times longer than wide. In cross section the anterior abdominal segments are roughly triangular (Fig. 2b), but posterior ones are more like squares, with each segment looking like a rectangular box (Figs 2c; 3c).

Table 1. Thoracic chaetal formulae in a sample of *Capitella caribaeorum* collected from southern Florida

Formula				No. of individuals
1–3c	4–9H			3
1–3c	4^{C}_{H}	5–9H		1
1–4c	5^{C}_{H}	6–9H		7
1–4c	$5–6^{C}_{H}$	7–8H	9^{G}_{H}	1
1–5c	6–7H	$8–9^{G}_{H}$		1
1–5c	6^{C}_{H}	7–9H		1
1–5c	6^{C}_{H}	7H	$8–9^{G}_{H}$	9
1–5c	$6–7^{C}_{H}$	$8–9^{G}_{H}$		2
1–6c	7H	$8–9^{G}_{H}$		2
1–6c	$7^{C'H}_{H}$	$8–9^{G}_{H}$		1
1–6c	7^{C}_{H}	$8–9^{G}_{H}$		5
1–7c	$8–9^{G}_{H}$			1

c, capillaries only in notopodia and neuropodia; H, hooded hooks only in notopodia and neuropodia; $^{C}_{H}$, capillaries only in notopodia, hooded hooks only in neuropodia; $^{C/H}_{H}$, mixed bundles of capillaries and hooded hooks in notopodia, hooded hooks only in neuropodia; $^{G}_{H}$, genital hooks only in notopodia, hooded hooks only in neuropodia.

Data on total length and chaetiger number are not included because some specimens had rear ends missing. It is important to note that the relative frequency of individuals with any particular chaetal formula will vary according to the age structure of the population. This table merely gives an indication of the range of formulae to be encountered in a sample of worms.

Chaetae are arranged in four widely-spaced bundles situated to the rear of each segment (Fig. 3c). In posterior segments the chaetae arise from glandular pads of which the neuropodial ones are more obvious (Fig. 1b). All abdominal segments normally bear chaetae (an average of two per bundle) except for developing segments in front of the pygidium (Fig. 3d). All abdominal chaetae are hooded hooks that are similar in structure to those found on the thorax.

The body terminates as a prominent glandular pygidium which takes the form of a swollen ring partly divided into two lobes by a posteroventral cleft containing the anus (Fig. 3d).

In gravid forms large yolky eggs are visible from segment 11. The number of ovigerous segments increases with age, ranging from eleven to thirteen. In young worms each ovary contains a single oocyte, but this number may increase to two or three in older worms. The species is hermaphroditic and under laboratory conditions is capable of self-fertilization (George, 1984).

Chaetal variation. George (1984) has traced the development of this species from larva to mature adult. At metamorphosis only the first 3 chaetigers have capillary chaetae; all others bear hooded hooks exclusively. At this stage there are 13 chaetigers. With increasing age capillaries gradually replace the hooks progressively backwards along the thorax. When the worms reach the 27–33 chaetiger stage there are only capillaries on segment 5, with mixed bundles of capillaries and hooded hooks on segment 6 and sometimes segment 7. At about this stage the genital hooks begin to develop and eventually the notopodial hooded hooks of segments 8 and 9 drop out.

Table 1 records the range of thoracic chaetal formulae of a field sample of 35 worms. The table gives some indication of the variation likely to be encountered in a natural population of this species. Such variability makes the use of thoracic chaetal formulae as a character for identification purposes very unreliable if used in isolation. However, there is a clear relationship between

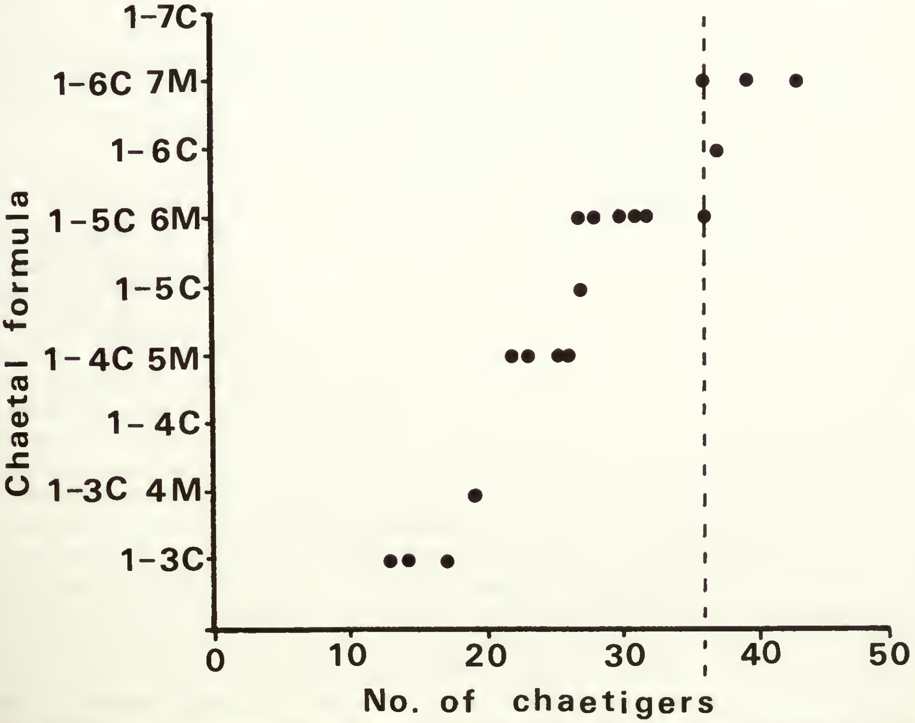

Fig. 4. Relationship between thoracic chaetal formula and chaetiger number in a sample of complete specimens. C—segment with capillaries only; M—segment with capillaries and hooded hooks. George (1984) found that no worms with fewer than 36 chaetigers were gravid. The 36-chaetiger point is indicated by a dotted line in the figure.

thoracic chaetal formula and total number of chaetigers as can be seen by analysis of a sample of complete worms (Fig. 4). Whenever possible, therefore, identifications should be based on a large sample of worms, including many complete individuals, and the relationship between thoracic chaetal formula and total chaetiger number checked against Fig. 4.

Discussion

Four genera of capitellids with nine thoracic chaetigers and genital hooks have been described. Of these *Branchiocapitella* Fauvel, 1932 is readily distinguished by the presence of cirriform branchiae. Warren (1976) referred *Capitellides* Mesnil, 1897 to the genus *Capitella* Blainville, 1828. *Capitellides* had been distinguished principally by the presence of genital hooks in both sexes. The description of *Capitomastus* Langerhans, 1880 is also very similar, but it includes reference to sexual dimorphism in the thoracic chaetal formula. The relationships of these three genera are very uncertain and a reappraisal of the *Capitella/Capitellides/Capitomastus* complex is currently under investigation by one of us (LMW).

Capitella caribaeorum appears to have many morphological and developmental features in common with *Capitomastus minimus sensu* Hauenschild (1954) collected from Rhodes in the Mediterranean. In the absence of either a detailed description or reference material it is impossible to draw any firm conclusion as to the status of this material.

Four species of *Capitella* with genital hooks in ovigerous individuals have been described. Of these *Capitella* (=*Capitellides*) *jonesi* (Hartman, 1959) and *Capitella* (=*Capitellides*) *teres* (Treadwell, 1939) have been recorded from the Caribbean province. Neither of these, however, could be confused with *C. caribaeorum* as they have different thoracic chaetal formulae: in *C. caribaeorum* the capillary chaetae occur in the first six or seven segments, whereas in *C. jonesi* they are restricted to the first three segments and in *C. teres* are present on the first eight segments.

In *Capitella hermaphrodita* Boletzky and Dohle, 1967 not all adults possess genital hooks and there are indications of a sex change from female to male (Warren, 1976). In *C. caribaeorum* the male reproductive system develops in advance of the female (George, 1984). Furthermore, capillary chaetae occur only on the first four chaetigers in *C. hermaphrodita*.

C. caribaeorum is most similar to *Capitella* (=*Capitellides*) *giardi* which was first described from the northern coast of France. The thoracic chaetal formula of this species is $1\text{–}6\mathrm{C}\ 7\mathrm{H}\ 8\text{–}9^{\mathrm{G}}_{\mathrm{H}}$, although capillaries are sometimes present in segment 7, giving it an identical formula to that of *C. caribaeorum*. *C. caribaeorum* differs most markedly in the number of hooded hooks, having on average 3 hooks per bundle in the thorax and 2 per bundle in the abdomen, whereas *C. giardi* has 4–5 hooks per bundle in the thorax and 7–10 per bundle in the abdomen. Adult *C. giardi* are slightly smaller than *C. caribaeorum* (Mesnil quoted a length of 10 mm) with a comparable number of chaetigers (35–45) so these differences cannot be attributed to size variations. Like *C. caribaeorum*, *C. giardi* produces a few large eggs. Mesnil (1897) quoted a dimension of 500 μm and Day (1937) gave a range of 290–370 μm for the largest dimension, compared with an average of 300 μm for *C. caribaeorum* (George, 1984). Although the egg sizes are similar, Day, in his description of the development of *C. giardi*, reported that at metamorphosis larvae had the first three segments with capillaries followed by thirteen segments with hooks. *C. caribaeorum*, on the other hand, has three segments bearing capillaries followed by ten hooked segments at metamorphosis (George, 1984). There is no evidence in the literature that *C. giardi* is hermaphroditic.

There are marked ecological differences between these two species. Mesnil found *C. giardi* in the intertidal zone at Wimereux in sediment covering clayey rock accompanied by *Polydora ciliata* (Johnston, 1838), *Pygospio elegans* Claparède, 1863 and *Fabricia sabella* (Ehrenberg, 1837), and amongst a thick encrustation of *Lithothamnion polymorphum* (Linnaeus) in rock pools in the granite bedrock at St Martin's Bay near to Cap de la Hague (n.b. It is unlikely that the species forming encrustations was *L. polymorphum* as stated by Mesnil. It is more likely to have been *Lithophyllum incrustans* Philippi). This is in marked contrast to the habitat of *C. caribaeorum* amongst decaying mangrove leaves.

George (1975) investigated the effects of temperature on the development of *C. caribaeorum* and found that 10°C was near the lower lethal limit for the species. At 15°C adults survived, but larvae did not develop beyond metamorphosis. The occurrence of *C. giardi* on the north coast of France indicates that this species survives far lower temperatures in the winter months.

In view of the apparent physical similarity between the species we attempted to obtain the type material of *C. giardi*, but this could not be traced. We made collections at both of its type localities in order to try to obtain specimens for comparison with *C. caribaeorum* but were unsuccessful.

Differential diagnosis

Capitella caribaeorum sp. nov. may be distinguished from the other species in the genus by the following characters: length 20 mm; 50 chaetigers; thoracic chaetal formula $1\text{–}6\mathrm{c}\ 7^{\mathrm{C}}_{\mathrm{H}}\ 8\text{–}9^{\mathrm{G}}_{\mathrm{H}}$; average of 3 chaetae per bundle in thorax, 2 per bundle in abdomen; hermaphroditic; habitat—decaying mangrove leaves; distribution—Caribbean province.

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References

Banse, K. 1970. The small species of *Euchone* Malmgren (Sabellidae, Polychaeta). *Proceedings of the Biological Society of Washington* **83:** 387–408.

Day, J. H. 1937. The development of *Capitellides giardi* Mesnil. *Report of the Dove Marine Laboratory* **4:** 31–37.

George, J. D. 1975. The culture of benthic polychaetes and harpacticoid copepods on agar. *10th European Symposium on Marine Biology, Ostend, Belgium, Sept. 17–23, 1975* **1:** 143–159.

—— 1984. The behaviour and life history of a mangrove-dwelling capitellid (Polychaeta). *In*: Hutchings, P. A. (Ed.) *Proceedings of the First International Polychaete Conference*. Sydney (The Linnean Society of New South Wales): 323–337.

Hauenschild, C. 1954. Über Sexualität und Entwicklungszyklus von *Capitomastus minimus*. *Zoologische Jahrbücher* **65:** 54–58.

Mesnil, F. 1897. Note sur un Capitellien nouveau (*Capitellides* n. gen., *Giardi* n. sp.). *Zoologischer Anzeiger* **20:** 441–443.

Warren, L. M. 1976. A review of the genus *Capitella* (Polychaeta: Capitellidae). *Journal of Zoology* **180:** 195–209.

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Relationships of the laticaudine sea snakes (Serpentes: Elapidae: Laticaudinae)

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Introduction

The genus *Laticauda* is considered by some workers to constitute the most primitive group of the sea snake family Hydrophiidae. However, others consider that *Laticauda* (Laticaudinae) and the true sea snakes (Hydrophiinae) are more likely to have had separate origins within the front-fanged proteroglyphous snakes (family Elapidae).

The paper considers morphological evidence for the relationships of laticaudines at a number of levels. Firstly, variation within the currently recognized species of *Laticauda* is discussed and clinal variation within the wide-ranging forms *L. laticaudata, L. colubrina*, and *L. semifasciata/schistorhynchus* is reviewed. The status of *L. crockeri,* a form endemic to a brackish water lake on Rennell Island (Solomon Islands), is considered and its relationships with *L. laticaudata,* to which it is sometimes regarded as being only subspecifically related, are discussed. Next, the relationships between *Laticauda* species are analysed using both phenetic and phylogenetic methods of analysis. In terms of overall (phenetic) resemblance, *L. colubrina* is closer to the *L. laticaudata/crockeri* lineage than to the divergent *L. semifasciata/schistorhynchus* lineage. Under phylogenetic analysis however, *L. colubrina* emerges as being somewhat transitional between the two lineages. Finally, the wider relationships of *Laticauda* are investigated, again using both phenetic and phylogenetic methods. *Laticauda* clearly shares more overall similarity with terrestrial elapines than with the hydrophiine sea snakes examined. However, when the same data are subjected to phylogenetic analyses (parsimony and compatibility methods) a rather conflicting picture emerges, but, in spite of the incompatibilities, the balance of evidence seems to support the hypothesis of comparatively close association between laticaudines and hydrophiines (a scheme that is also congruent with recent immunological studies).

Malcolm Smith (1926: xi), in his classic work on sea snakes (Hydrophiidae), regarded *Laticauda* as the most primitive sea snake genus and suggested a dual origin of the Hydrophiidae; the Laticaudinae (in which he placed *Laticauda, Aipysurus* and *Emydocephalus*) from Australia and the Hydrophiinae (containing the remaining sea snakes) from Indo-Malaya. Later he appeared to slightly modify his opinion by stating (Smith 1943: 439) that the Laticaudinae and Hydrophiinae 'are united through *Ephalophis*'. Underwood (1967: 110) however mentioned that à case still had to be made that *Laticauda* is related to the other sea snakes and McDowell (1967, 1969, 1972, 1974) has argued that *Laticauda* is not closely related to the true sea snakes (Hydrophiinae including *Aipysurus* and *Emydocephalus)* but represents an independent marine adaptation of a group of elapids comprising the Asiatic coral snakes (*Calliophis, Maticora*), the American coral snakes (*Micrurus* and *Micruroides*) and an elapid from Bougainville, Solomon Islands *(Parapistocalamus).*

Some workers have accepted McDowell's theory, for example Smith *et al.*(1977) even proposed a radical change in classification with *Laticauda* being placed in the subfamily Elapinae of the family Elapidae and remaining sea snakes being assigned to the subfamily Hydrophiinae of the family Hydrophiidae. Others have, however, regarded the position of *Laticauda* as equivocal e.g. Voris (1977) grouped *Laticauda* and true sea snakes together in the same family (Hydrophiidae) but stated that *Laticauda* is 'a group of very closely related species distinct from all other sea snakes and either represent an independent evolutionary line or a very early separation from all other sea snakes'.

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Recent immunological evidence (e.g.Cadle & Gorman, 1981; Mao *et al.*, 1983) suggests that *Laticauda* and true sea snakes are relatively closely related although Mao *et al.* (1983: 870) state that 'the Hydrophiinae are much closer immunologically to the Australian elapids than is the genus *Laticauda*'.

In the belief that this somewhat confused picture could possibly be clarified by phylogenetic methods of analysis, the author undertook a study of the morphological characters which bear upon the relationships of *Laticauda* (McCarthy, 1982). While no very clear answer to the central problem was obtained the resulting data set has a number of interesting aspects which are presented here.

Intraspecific variation in *Laticauda*

The genus *Laticauda* has an extensive distribution from the Bay of Bengal through the Indo-Australian area, north to Japan and west to some South Pacific islands (Niue, Tonga and Samoa); there are even unconfirmed reports of the occurrence of one species on the west coast of Central America (Fig. 1).

Five species are currently assigned to the genus although two of these (*L. crockeri* and *L. schistorhynchus*) are regarded by some authorities as being only subspecifically distinct. Two of the species (*L. laticaudata* and *L. colubrina*) together occupy almost the entire known range of the genus. *L. semifasciata* and *L. schistorhynchus* appear very closely related to each other but have peculiarly disjunct distributions (see below). *L. crockeri*, a close relative of *L. laticaudata*, is confined to a land-locked lagoon on Rennell Island, Solomons.

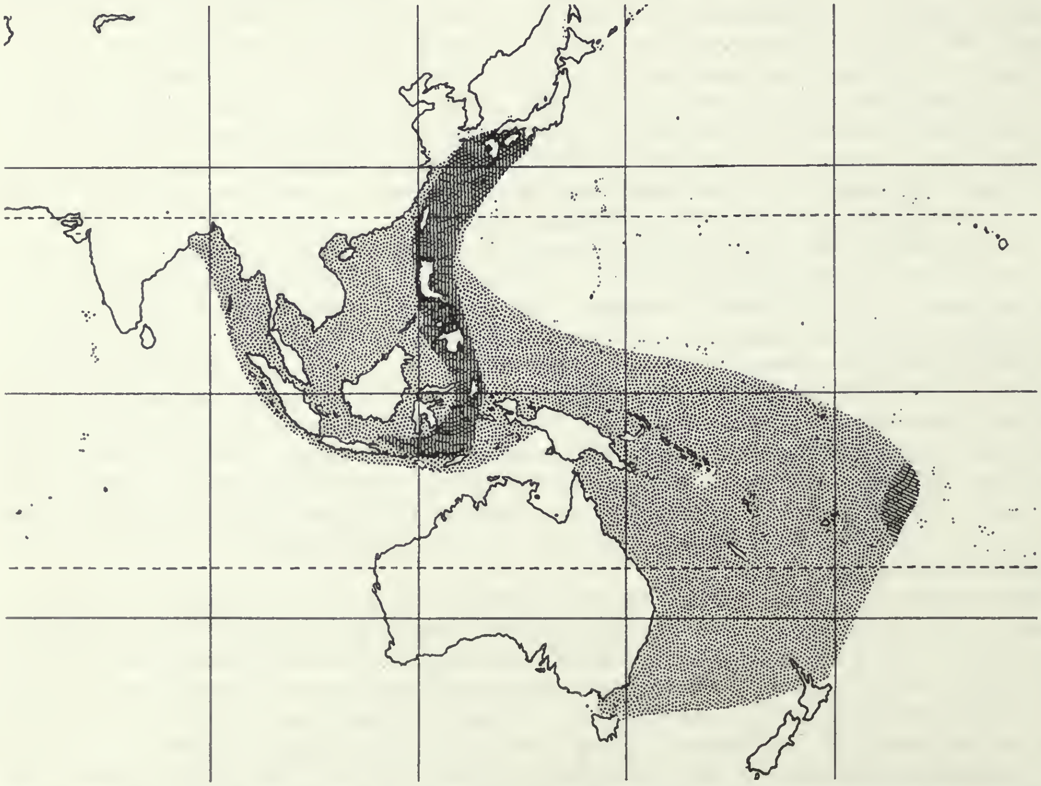

Fig. 1 Distribution of laticaudine sea snakes. Stippled shading = Joint distributions of *Laticauda colubrina* and *L. laticaudata* (there are also some reports of *L. colubrina* from Central America, p. 134). Vertical line shading = Distribution of *L. semifasciata*. Oblique line shading = Distribution of *L. schistorhynchus*. Asterisk = Distribution of *L. crockeri*.

Laticauda laticaudata (Linnaeus, 1758)

A wide-ranging species regarded (e.g. Klemmer, 1963) as comprising two subspecies:- *L. l. laticaudata* (Linnaeus, 1758) from Philippines, Indo-Australian Archipelago, New Guinea, Australia, Oceania and *L. l. affinis* (Anderson, 1871) from India, Malay Peninsula, South China, Taiwan and Ryukyu Retto (Japan).

According to Stejneger (1907: 404) the two forms may be distinguished on colour pattern. *L. laticaudata laticaudata* has a light horse-shoe shaped mark, on top of the head, which bends down behind the eye to reach the lip. In contrast, the light horse-shoe shaped mark in *L. laticaudata affinis* does not curve down behind the eye (Fig. 2). Additional differences between the two forms, cited by Stejneger, include: light coloured rings on belly 4–5 ventrals wide in *L. l. laticaudata* which also has no or one incomplete light ring on the neck; in *L. l. affinis* the light belly rings are 1–3 ventrals wide and there are usually two incomplete light neck rings. Stejneger also commented that the extent to which these characters held good in a large series required investigation.

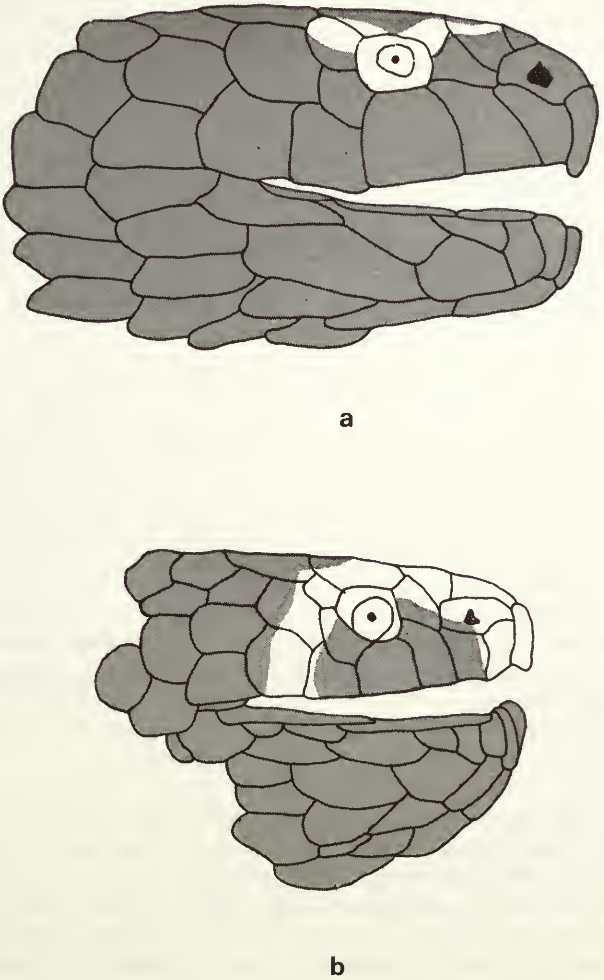

Fig. 2 Head coloration in *Laticauda laticaudata*. (a) Typical 'eastern' form (Loo Choo); note that the light mark does not turn down posterior to the eye. (b) Typical 'western' form (Tasmania); note the down-turned light mark.

Table 1. *Laticauda laticaudata*, geographical variation.

Registration number[1]	Locality	Down-turned head-mark[2]	Incomplete neck rings	Number of ventrals in light ring
BM 56·9·4·53	Fiji	+	0	2·3–2·9
BM 77·2·24·18	Duke of York Id.	+	0	3·4–4
BM 1926·11·1·6	Java	+	0	5–5·6
BM 42·11·22·34	New Guinea	+	0	3–3·2
BM 55·11·7·31	San Cristobal	+	0	3·4–3·7
BM 55·10·16·439	Tasmania	+	1	2·7–2·9
BM 59·9·20·70	'Chartaboum' (locality suspect)	+	1	3·2–3·8
BM 1966·309	Aneitum, New Hebrides	+	0	2·7–2·8
BM 1936·2·1·17	Florida, Solomons	+	0	3·6–4·1
BM 42·11·22·32	New Guinea	+	0	2·9–3·5
ZMC 66265	Sydney	+	0	3·5
RML 6272	Ternate	+/−	2	1·95–2·75
RML unreg.	Deli	+/−	1	1·8–2
ZMC 66262	Nicobar	−	2	3–3·5
ZMC 66263	Nicobar	−	2	2·7–3·2
BM 1925·12·8·2	Bengal	−	1	4–4·7
BM 1901·10·23·9	Ishigahi, Loo Choo	−	1	1·4–1·7
BM 87·1·31·36	Loo Choo	−	2	0·3–1·8
RML unreg.	Sika	−	2	2–3
RML 6274a	Menado	−	2	2–2·3
RML 6274b	Menado	−	2	2·5
RML 5898a	Sulawatti	−	2	2·5–2·8
RML 5898b	Sulawatti	−	2	2·0–2·6
RML 10668	Pasir	−	2	1·7–2·2
RML 5503a	Nias	−	2	2·3
RML 5503b	Nias	−	2	1·95–2·2
RML 12628	Ambon	−	1	3·5–4
RML 10669	Soek	−	2	1·7–1·9
RML 7590	Atjeh	−	1	2·2–2·8
RML 12663	Laboean Lembeh	−	2	?
RML 6271	Ambon	−	2	2·2–2·6
RML 12649	Obi	−	2	2–2·5
RML 5218a	Sumatra	−	2	2–2·6
RML 5218b	Sumatra	−	2	2–2·5

[1] BM = British Museum (Natural History), London; RML = Rijksmuseum van Natuurlijke Historie, Leiden; ZMC = Zoologisk Museum, Copenhagen.

[2] + indicates presence; − indicates absence.

Table 1 shows the distribution of the above characters in the 34 specimens of *L. laticaudata* examined in the present study. It appears that the head pattern can indeed be used to partition *L. laticaudata* broadly into eastern and western populations however some specimens in the intermediate area (Ternate and Deli) show asymmetry, the head mark being down-turned on one side of the head but not on the other. Additional features do not correlate *absolutely* with the condition of the head mark but there is a degree of correspondence; 8 of the 13 specimens that show some down-turning of the head mark also have light body rings that are in excess of three ventrals wide whereas only 3 of the 21 specimens that lack the down-turning have light bands as broad as this. Additionally the number of incomplete neck bands is generally greater in eastern than in western specimens (17 of the 21 eastern forms have two incomplete neck rings whereas none of the 11 western forms have this condition; the intermediate specimens from Ternate and Deli have two and one incomplete neck rings respectively). If subspecies of *L. laticaudata* are deemed worthy of recognition, which seems unwarranted owing to the apparently clinal nature of the variation between eastern and western forms, Enderman (1970 unpublished ms.) observes that Linnaeus's type of *laticaudata* was probably based on an Asiatic specimen; he would therefore relegate *affinis* (Anderson, 1871) to the synonymy of *L. l. laticaudata*. In this event the name available for the Pacific population appears to be *L. l. muelleri* (Boulenger, 1896).

Laticauda crockeri Slevin, 1934

Endemic to Lake Tegano (= Te-Nggano), Rennell Island, this species resembles *L. laticaudata* in several respects. The main points of difference between the two forms are outlined below:

L. crockeri	*L. laticaudata*
1. Midbody scale rows 19; occasionally 21	1. Midbody scale rows invariably 19
2. Ventral scales 192–207	2. Ventral scales 219–252
3. Strong but variable tendency to melanism; some individuals almost uniformly dark.	3. Not melanistic, head pattern and body banding always clearly visible.

Slevin's (1934) description of *L. crockeri* was based on one uniformly dark brown specimen, with 21 midbody scale rows, collected in Lake Tegano in 1933. In 1956, Volsøe described a new subspecies from the lake, *L. laticaudata wolffi* based on three individuals all with 19 midbody scale rows and with a degree of melanism i.e. 'head entirely black above and dark brown below' ground colour of body 'dark slate grey dorsally (almost merging with the black bands)'. He further noted that *L. laticaudata wolffi* appeared to differ from Slevin's description of *L. crockeri* in only two respects:- in the number of scale rows (19 vs. 21) and in coloration. In addition, Volsøe reported that *L. colubrina* also occurred in the lake. He therefore described the following situation:

> This freshwater lake is inhabited by no less than three different species of sea snakes all belonging to the same genus *Laticauda* namely:
> 1. *L. colubrina*. The lake population is undifferentiated from the typical form which occurs also along the shores of the island.
> 2. *L. laticaudata wolffi*. Subspecifically distinct from the nominate form which has not been taken from the shores of Rennell Island ...
> 3. *L. crockeri*. An endemic species with unknown relationships to other species of *Laticauda*.

Later, Volsøe (1958) described nine further specimens of *L. 'laticaudata'* from the lake. He recorded that eight had 19 midbody scale rows (like *L. l. wolffi*) whereas one had 21 midbody scale rows reducing to 19 a little distance posteriorly. The aberrant specimen was very dark (and therefore in agreement with the description of *L. crockeri*) but three of the other specimens matched it in colour. He concluded that 'there can be no doubt, therefore, that they all belong to the same form'. The correct name to be applied to the Lake Tegano endemic, following Volsøe (1958) is *L. laticaudata crockeri* with *L. l. wolffi* being reduced to a synonym of that form.

Recently, Cogger (1975: 124) implied that the status of *L. laticaudata wolffi* and *L. crockeri* was uncertain, citing a suggestion by Voris (1969 unpublished thesis) to the effect that '*wolffi* may represent the product of recent hybridization between *crockeri* and immigrant *laticaudata*'. Kharin (1984) treats *L. laticaudata wolffi* and *L. crockeri* as separate entities. However, McCoy (1980: 70) is of the opinion that '*crockeri* and *laticaudata wolffi* are almost certainly synonymous'.

Wolff (1969, 1970) agreed with Volsøe and recognized only two forms from the lake; *L. laticaudata crockeri* and *L. colubrina*. He commented that whilst the lake population of *L. colubrina* appears indistinguishable from individuals occurring outside the lake, '*L. crockeri* has become clearly differentiated from the ancestral form' (Wolff, 1970: 20), suggesting that either *L.*

colubrina is a recent invader or 'for some unknown reason is the only one of the two species which migrates to and from the lake through the subterranean channel'.

Among a large series of *crockeri* collected by him in 1977, McCoy (1980: 70) found that 'most specimens had 19 scale rows at midbody, several had 21 and one individual had 19, 20 and 21 rows in an area around midbody', moreover 'there was no relation between the number of scale rows and the degree of distinction of the dark banding'. In the present study of relatively large series of *Laticauda crockeri* has been examined in the collection in the Zoologisk Museum, Copenhagen (including the holotype and paratypes of *L. l. wolffi*.). The holotype of *L. crockeri* (from the California Academy of Sciences) and a paratype of *L. l. wolffi* in the British Museum (Natural History) have also been available. Table 2 displays the distribution of the supposed diagnostic features of *L. crockeri* and *L. l. wolffi* in this sample. It can be seen that a midbody count of 21 is uncommon (occurring in 2 out of 19 specimens) in the sample of *crockeri* examined. That it is also aberrant is indicated by the complex scale row reduction formulae (given below) of the two specimens recorded as having this count:

Scale row reduction formula of *L. crockeri* (HOLOTYPE) CAS 72001

$$20\,\frac{}{5+6\ (\text{before first ventral})}\,19\,\frac{6=6+7(82)}{5=5+6(82)}\,21\,\frac{6+7(83/84)}{6+7(84)}\,19$$

$$19\,\frac{5=5+6(92),\ 6+7(94),\ 5=5+6(97)}{5=5+6(88),\ 6+7(90),\ 5=5+6(96)}\,21\,\frac{}{6+7(100)}\,20\,\frac{}{5=5+6(103)}\,21$$

$$21\,\frac{6+7(104)}{}\,20\,\frac{5=5+6(108)}{}\,21\,\frac{6+7(112)}{}\,20$$

$$20\,\frac{5=5+6(115)}{}\,21\,\frac{5+6(118)}{}\,20\,\frac{5=5+6(120)}{}\,21$$

$$21\,\frac{6+7(127)}{6+7(126)}\,19\,\frac{5+6(189)}{4+5(188)}\,17\,\frac{v=2(196)\ 4+5(200)}{2=2+3(202)}\,18$$

Scale row reduction formula of specimen ZMC 66134

$$21\,\frac{6+7(108)}{}\,20\,\frac{5=5+6(110)}{}\,21\,\frac{6+7(119),\ 5=5+6(120),\ 6+7(124)}{6+7(124)}\,19$$

$$19\,\frac{}{4=4+5(129)}\,20\,\frac{}{6+7(131)}\,19\,\frac{}{5=5+6(134)}\,20\,\frac{}{6+7(139)}\,19$$

$$19\,\frac{4+5(187)}{4+5(191)}\,17\,\frac{}{3+4(202)}\,16$$

The marked irregularity of the above formulae together with the rare occurrence of 21 midbody scale rows is strong evidence for the atypical nature of the condition.

Complete melanism is also rather rare and not necessarily correlated with the number of midbody scale rows (McCoy, 1980). It seems certain that Volsøe (1958) was correct in regarding *L. crockeri* and *L. l. wolffi* as synonyms.

Whether to treat the endemic form as being only subspecifically distinct from *L. laticaudata* is problematical. *L. laticaudata* and *L. crockeri* certainly resemble each other rather closely in many features that are not shared with other *Laticauda* species e.g. azygous prefrontal scale is absent; first rank of marginal lower lip scales is elongate; usually 19 midbody scale rows; heart tip in a more anterior position than *L. colubrina*; tracheal lung absent; vestigial left lung present (like all *L. laticaudata* and only some *L. colubrina*).

Table 2. *Laticauda crockeri*, scale row reduction and extent of melanism.

Registration number[1]	Abbreviated scale row reduction neck: midbody: vent	Degree of melanism head melanistic/ body melanistic[2]
CAS 72001 (Holotype of *L. crockeri*)	20(19) : 21 : 18	+/+
ZMC 668 (Holotype of *L. l. wolffi*)	19 : 19 : 17	+/−
ZMC 666 (Paratype of *L. l. wolffi*)	? damaged	+/−
ZMC 667 (Paratype of *L. l. wolffi*)	19 : 19 : 16	+/−
BM 1955·1·13·10 (Paratype of *L. l. wolffi*)	21 : 19 : 18	+/−
ZMC 66134	21 : 21 : 16	+/−
ZMC 66135	? damaged	+/+
ZMC 66136	21 : 19 : 16	+/−
ZMC 66137	21 : 19 : 16	−/−
ZMC 66138	19 : 19 : 15	+/+
ZMC 66139	19 : 19 : 17	−/−
ZMC 66140	19 : 19 : 17	−/−
ZMC 66141	19 : 19 : 15	−/−
ZMC 66142	21 : 19 : 16	−/−
ZMC 66293	19 : 19 : 15	−/−
ZMC 66294	21 : 19 : 16	−/−
ZMC 66244	21 : 19 : 17	−/−
ZMC 66245	21 : 19 : 15	−/−
ZMC 66239	19 : 19 : 16	−/−
ZMC 66240	19 : 19 : 17	−/−
ZMC 66237	19 : 19 : 15	−/−

[1] BM = British Museum (Natural History), London; CAS = California Academy of Sciences, San Francisco; ZMC = Zoologisk Museum, Copenhagen.

[2] + = complete melanism; − = head pattern or body bands visible.

Most of the above characters appear to be relatively primitive and therefore unlikely to be strong indicators of close relationship. However it is also true that very few characters have yet been discovered that can effectively discriminate between *laticaudata* and *crockeri*; only the ventral count seems entirely to do so (192–210 in *crockeri*, 219–252 in *laticaudata*). Additionally, Tamiya, *et al.* (1983), in their analysis of neurotoxins, found that '*L. laticaudata* and *L. crockeri* are very closely related, although there are some genetic differences'. It seems therefore reasonable to suggest that *L. laticaudata* and *L. crockeri* are more closely related to each other than either is to any other extant species. *L. crockeri* may only be a subspecies of *L. laticaudata* but as the forms are allopatric this hypothesis is difficult to confirm.

Voris's (1969: 368–369) hypothesis that an invasion of *L. laticaudata* resulted in hybridization between it and *L. crockeri* to produce *L. laticaudata wolffi* is hardly supported by the evidence. Perhaps the most likely explanation for the situation in Lake Tegano is that a population (possibly of *L. laticaudata*) became isolated when the lake was formed. According to Wolff (1970: 20) the age of the lake as a brackish water body is unknown, 'although it seems probable that the lagoon was cut off from the sea not long after the elevation of the land started in the late Pliocene'. *L. crockeri* may have evolved its pecularities as a result of: selection processes in the lake environment, inheritance from a somewhat aberrant founder population, or genetic drift due to isolation in a small population.

An enigma still remaining to be considered is: why has the *crockeri* population in the lake become distinct whereas *L. colubrina* appears not to have formed a discrete lake form? As mentioned earlier, Wolff (1970) suggests that *crockeri* is unable to navigate through an inferred subterranean passage to the sea whereas *colubrina* is able to do so. However, a simpler explanation is afforded by knowledge of *L. colubrina*, a species that appears to be more terrestrial in its habits than other species of *Laticauda*. This suggests that *L. colubrina* may be able to cross the high ground surrounding the lake and thus maintain genetic flow with the marine population. Wolff (1970: 13) observes that the lake is 'surrounded on all sides by a rim with a width of 0·9–2 km and a continuous height of about 100 m'; the only exception is at the extreme eastern end of the lake where the height of the rim is only 45 m.

The climbing ability of *L. colubrina* is demonstrated by a record of some specimens from Taiwan that were found on top of a solitary coral reef about 50 m high (Mao & Chen, 1980). Although *L. crockeri* 'has been found moving amongst short grass surrounding the lake' (McCoy, 1980: 70) it may be less terrestrial in its habits than *L. colubrina* and a barrier of the dimensions described by Wolff might well prevent it commuting between the lake and the sea.

Laticauda colubrina (Schneider, 1799)

This species has a very widespread distribution which is largely shared with *L. laticaudata*. Additionally there are some reports of *L. colubrina* from Nicaragua (Villa, 1962), Mexico (Alvarez del Toro, 1982) and El Salvador (Villa, pers. comm.). Unfortunately these records are based on material that is no longer available for examination; the presence of *L. colubrina* in tropical America therefore requires substantiation (Villa, pers comm.).*

Through its range, *L. colubrina* shows considerable variation in neck and body coloration and in some aspects in its scalation. Enderman (1970) considers that six populations of *L. colubrina* are worthy of subspecific recognition: (i) New Caledonia; (ii) Fiji, Tonga, Society Islands; (iii) New Hebrides (=Vanuatu), Solomons, Bismarck Archipelago; (iv) Geelvink Baai (northern Irian, New Guinea); (v) Lesser Sunda Islands and S.W. New Guinea to Ryukyus, Japan; (vi) Sumatra, Malaya, Bay of Bengal. The features which Enderman cites to support the recognition of these subspecies comprise mainly relatively minor differences in neck and body banding; he also observes that populations (i)–(iv) usually lack a postmental scale whereas populations (v) and (vi) normally have one (Fig. 3).

Amino acid sequencing of neurotoxins reveals at least three genetically different populations of *L. colubrina*: the difference in the structure of long-chain neurotoxins, between populations from Japan and the Philippines in contrast with those from the Solomons, Fiji and New Caledonia, is

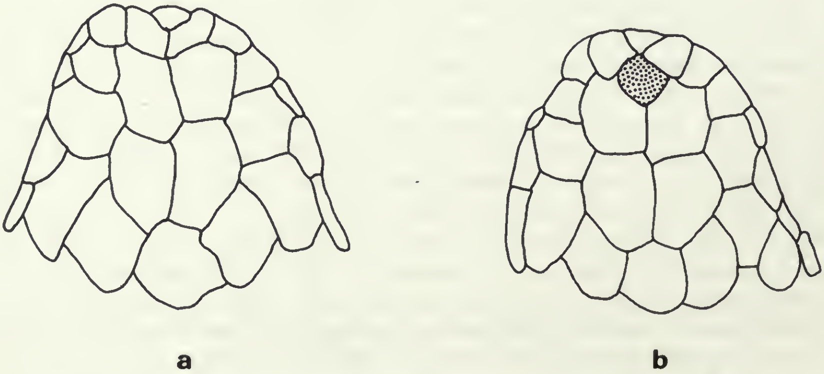

Fig. 3 Chin shields of *Laticauda colubrina*. (a) Typical 'western' form (Solomon Is); postmental scale absent. (b) Typical 'eastern' form (Singapore); postmental scale present (stippled).

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*A female specimen in Stuttgart Museum (SMNS-4203) is alleged to have been collected in Guatemala in 1877 (donor unknown); the collecting locality is thought doubtful (Wermuth & Schluter, pers. comm.). In most respects the specimen appears to be a fairly typical western form having a fairly low ventral count (226) and lacking a postmental scale. It has one incomplete light band on its neck and 28 dark bands on its body.

especially well-marked (Tamiya *et al*., 1983). Very recently a population in Vanuatu, with low ventral scale count and unusual neck coloration, has been studied, which appears to be a distinct species, occurring sympatrically with more typical *L. colubrina*. A related population occurs in the northern part of the Tonga island group (Cogger, pers. comm.).

A full analysis of population variation in *L. colubrina* is beyond the scope of the present study. However, examination of some morphological characters of 72 specimens (Table 3) indicates that, like *L. laticaudata,* the main division appears to be into eastern and western forms. The trend in ventral counts of *L. colubrina* is for them to be generally higher in eastern specimens than western specimens. This tendency in ventral counts is also reflected in some *L. colubrina* literature records. Guinea (1981), for instance, give mean ventral counts of 223 (n = 6) and 228·7 (n = 10), for males and females respectively, from Fiji, whereas Mao & Chen (1980) give mean counts of 231 (n = 9) and 236 (n = 16), for males and females respectively, from Taiwan.

Some other characters are only variably present in *L. colubrina* i.e. azygous prefrontal scale and vestigal left lung, but these features appear to show no obvious correlation with geographic distribution.

Table 3. *Laticauda colubrina*; geographical variation in the ventral counts and in postmental presence.

Locality	Sex	n	Ventrals range (mean)	Postmental percentage presence
Japan	♀	1	249·5	100%
Taiwan	♂	1	239	100%
Philippines	♂	1	236	100%
	♀	1	249	100%
Malaya & Thailand	♂♂	6	224–240·5 (233·75)	66·7%
	♀♀	5	234–248 (243·4)	60%
Andamans	♀	1	235	100%
Sumatra	♂♂	3	223–224 (223·33)	66·7%
	♀	1	240	100%
Borneo	♂	1	230	0
Java Sea	♀	1	227	100%
Sulawesi	♂	1	228	100%
	♀	1	232	100%
Moluccas	♂	1	226	100%
	♀	1	238	100%
Lesser Sunda Is.	♂♂	2	226–228 (227)	50%
	♀	1	234	100%
New Guinea	♂♂	3	232–240·5 (235·17)	66·7%
	♀♀	3	229–240 (235)	100%
Solomon Is.	♂♂	9	218–229 (222)	0
	♀♀	12	220–233 (226·79)	0
New Caledonia	♂	1	221	0
	♀	1	224	0
New Hebrides[1]	♂♂	3	216–225·5 (219)	0
	♀	1	213	0
Fiji & Tonga	♂♂	4	224–226 (225)	0
	♀♀	3	229–236 (232·67)	0
Australia & New Zealand	♂♂	2	214·5–219 (216·75)	0
	♀	1	231	0

[1] Two distinct forms are recorded from New Hebrides (= Vanuatu), one ('new form') with low ventral count and unusual neck coloration, the other with higher ventral counts and more typical *colubrina* coloration (Cogger, pers. comm.). The ♂ with 216 ventrals and the ♀ with 213 ventrals, in the above series, appear assignable to this 'new form'.

Laticauda semifasciata (Reinwardt in Schlegel, 1837) and *Laticauda schistorhynchus* (Günther, 1874)

L. semifasciata and *L. schistorhychus* closely resemble each other, indeed they mainly appear to have only *average* differences, i.e. number of ventrals and bands on the body and in maximum adult size (Smith, 1926).

Tamiya *et al.* (1983: 447) analysed neurotoxins and found that *L. semifasciata* and *L. schistorhynchus* are genetically homogeneous as far as these components are concerned. Guinea, Tamiya & Cogger (1983) concluded that there is no justification for treating *L. semifasciata* and *L. schistorhynchus* as separate species.

There do indeed seem reasonable grounds for considering the two forms conspecific. However, there is no proof that they interbreed; *L. semifasciata* and *L. schistorhynchus* are completely allopatric being separated by an enormous gap. *L. semifasciata* has been recorded from South Japan, Riu Kius, Philippines, Moluccas and Lesser Sunda Islands, whereas *L. schistorhynchus* is found in the Pacific at Niue, Tonga and Samoa. There is however a single dubious record of *L. schistorhynchus* from 'Bertrand' Island (= Tendanye Island), New Guinea (a specimen in the Hamburg Museum cited by Smith 1926).

The circumstances that led to splitting of *L. semifasciata/schistorhynchus* populations are unknown but it is possible that competition from similar forms might, at least in part, be responsible. In the area where members of the *semifasciata* group are absent, for instance, there occur members of the genus *Aipysurus*. *Aipysurus* comprises several species of hydrophiines that are confined (with the exception of *A. eydouxi*) to the continental shelf waters of Australia and New Guinea, they also occur in parts of the extreme south west Pacific Ocean (Cogger, 1975: 72). This diversity of shallow-water sea snakes might well fill niches that are thus unavailable for the *semifasciata* group; this theory might also account for the relative rarity of other *Laticauda* species in Australian waters.

Characters examined—Data matrix

The Elapidae are a relatively large family (comprising 244 species according to Dowling & Duellman, 1978; McCarthy, 1985), therefore there are practical difficulties in examining all elapid species for many characters that might have relevance to the question of laticaudine relationship.

Table 4. Survey of *Laticauda* 'special features'.

	Character state numbers (derived conditions)[2]						
Group[1]	7·1 or 7·2	9	25·2	26·2 or 26·3	46·2	48	65
Laticauda	+	+	+	+	+	+	+
Hydrophiines	+	−	−	+	+	+	−
African & Middle Eastern elapines	+	−	+	−	−	−	−
Asiatic elapines	−	−	+	−	+	+	−
American elapines	−	−	+	+	+	−	−
New Guinea & Solomons elapines	−	−	+	+	−	−	−
Australian elapines	−	−	−	+	−	−	−

[1] + indicates the presence of a state in at least some members of the group concerned.

[2] Character states are described in Table 5.

In order to cope with this problem it was decided to carry-out methods of analysis on a sample comprising all species of *Laticauda* together with a selection of ten other elapids.

The non-laticaudines in the sample were selected on the basis of a survey of the Elapidae for seven characters of *Laticauda* that were hitherto believed to have a restricted distribution outside the genus. The results of the survey are summarised in Table 4. The resulting sample of elapids was then examined for 45 binary and 20 multistate characters (Table 5) and a data matrix was compiled (Table 7).

Polarity of the characters (Table 6) was mainly determined on the criterion of out-group comparison i.e. if a character state is common (widespread) among Caenophidia (higher snakes), it is regarded as primitive within the Elapidae. A more detailed account of the characters analysed, and polarity criteria used, is given by McCarthy (1982).

The problem of relationship is considered from a number of perspectives i.e. from the viewpoint of overall ('phenetic') resemblance (see Sneath & Sokal, 1973) and from the viewpoint of various phylogenetic ('cladistic' or 'evolutionary') approaches (see review by Felsenstein, 1982).

Two basic levels of affinity will be considered here: (*a*) The relationships of *Laticauda* species to each other. (*b*) The relationships of the genus *Laticauda* to other elapids.

Interspecific relationships within genus *Laticauda*

Phenetic analysis

Overall (phenetic) similarity can be measured in many ways; one of the most commonly used coefficients is the simple-matching coefficient and it is this expression of resemblance that is used here. Simple-matching coefficients are calculated (e.g. Sneath & Sokal, 1973: 132) according to the formula:

$$\mathrm{Ssm} = \frac{\mathrm{m}}{\mathrm{n}}$$

(where m = the number of matches between pairs of taxa and n = the number of characters)

The overall similarity matrix is shown in Table 8. From this the scheme illustrated in Fig. 4 was constructed using the 'unweighted pair-group' method of clustering (as discussed by Sneath & Sokal, 1973: 230–234).

From Figure 4 it can be seen that *Laticauda semifasciata* and *L. schistorhynchus* are very close to each other phenetically; similarly *L. crockeri* and *L. laticaudata* cluster together. *L. colubrina* resembles *L. laticaudata/crockeri* more than it does *L. semifasciata/L. schistorhynchus*. Overall, the topology is the same as in the phenogram presented by Voris (1977: 91) who also used simple matching coefficients on his data.

Phylogenetic analysis

Phylogenetic (cladistic) analysis involves considering the relationships between taxa in terms of shared derived characters ('synapomorphies'). Reference to the data matrix (Table 7) shows that, when only derived states are considered, there is a conflict between 9 states (7·2; 12·1; 29; 32; 56; 57·2; 58; 60; 64·2) supporting the association of *L. colubrina* with the *L. laticaudata* lineage and 4 states (1·1; 8·2; 14; 15) supporting the clustering of *L. colubrina* with the *semifasciata* lineage. The principle of parsimony ('democratic method' Arnold, 1981: 21) leads one to accept the scheme that is supported by most evidence i.e. the same topology as suggested by phenetic analysis (Fig. 4) with *colubrina* associated with *laticaudata* and *crockeri*. However 6 of the 9 states supporting this association have rather arbitrary polarity determinations (12·1; 29; 32; 58; 60; 64·2) and perhaps should not be used as primary evidence. If arbitrarily scored states are discounted, the balance of evidence shifts marginally in favour of a scheme associating *colubrina* with the *semifasciata* lineage. Two of the 4 states supporting the association of *colubrina* with *semifasciata* are variable the primitive state occurring in some individuals i.e. in *colubrina*, the azygous prefrontal

Table 5.

Summary of character states included in matrix				Additive binary codings (where relevant)	
1.1.	Azygous prefrontal shield	0	Absent		
		1	Present		
1.2.	Head shield fragmentation	0	Absent		
		1	Present		
2.	Horizontal division of rostral	0	Absent		
		1	Present		
3.	Nostril position	0	Lateral		
		1	Dorsal		
4.	Internasal scales	0	Present		
		1	Absent		
				5·1	5·2
5.	Anterior temporals	0	One or two	0	0
		1	None	1	0
		2	Three	0	1
				6·1	6·2
6.	Infralabial formula	0	7(4 + 3)	0	0
		1	6(4 + 2)	1	0
		2	8/9(4 + 4/5)	0	1
				7·1	7·2
7.	Marginal lower lip scales	0	None	0	0
		1	Present (one rank)	1	0
		2	Present (two ranks)	1	1
				8·1	8·2
8.	Scale rows (midbody)	0	14–21	0	0
		1	10–13	1	0
		2	c.21 or over	0	1
9.	Nasal vestibule	0	Smooth lining		
		1	Rugose/papillate lining		
10.	Tail shape	0	Rounded		
		1	Laterally compressed		
				11·1	11·2
11.	Heart position	0	19–28% ventral count	0	0
		1	29–32% ventral count	1	0
		2	> 33% ventral count	1	1
				12·1	12·2
12.	Heart-liver distance	0	> 6% ventral count	0	0
		1	4–5% ventral count	1	0
		2	< 4% ventral count	1	1
13.	Heart-systemic arch gap	0	< 2% ventral count		
		1	> 2% ventral count		
14.	Vestigial left lung	0	Present		
		1	Absent		
15.	Tracheal lung	0	Absent		
		1	Present		
				16·1	16·2
16.	Pulmonary air sac	0	Flimsy (not extending to cloaca)	0	0
		1	Muscular (not extending to cloaca)	1	0
		2	Muscular (extending within 5% ventral count from cloaca)	1	1
				17·1	17·2
17.	Liver size	0	< 23% ventral count	0	0
		1	23–29% ventral count	1	0
		2	> 40% ventral count	1	1

Table 5. *cont.*

Summary of character states included in matrix			Additive binary codings (where relevant)		
18. Liver: vena cava position	0	Central for at least short distance			
	1	Lateral			
19. Kidney: furthest extent	0	More posterior than 90% ventral count			
	1	Less than 90% ventral count			
20. Renal artery pattern	0	1 + 1			
	1	2 + 1 or greater			
			21·1	21·2	
21. Hemipenial calyces	0	Distal calyces	0	0	
	1	Distal & proximal calyces	1	0	
	2	Calyces absent	0	1	
			23·1	23·2	
23. Sulcus bifurcation	0	Significant	0	0	
	1	Only at tip of organ	1	0	
	2	Sulcus simple	1	1	
24. Hemipenis shape	0	Distinctly forked			
	1	Slightly bilobed or simple			
			25·1	25·2	
25. Venom gland shape	0	Rounded; confined to temporal area	0	0	
	1	Extends posteriorly into the body cavity	1	0	
	2	Down-turned posterior corner	0	1	
			26·1	26·2	26·3
26. 'Superficialis' muscle origin	0	Narrow	0	0	0
	1	Broad (not reaching quadrate)	1	0	0
	2	Broad (attaching onto quadrate)	1	1	0
	3	Quadrate head isolated from rest of muscle	1	1	1
27. 'Superficialis' muscle (interruption)	0	Passes uninterrupted around venom gland			
	1	Divided into dorsal and ventral portions			
			28·1	28·2	
28. 'Superficialis' muscle (aponeuroses)	0	No aponeurotic origin	0	0	
	1	Narrow aponeurotic origin	1	0	
	2	Broad aponeurotic origin	1	1	
29. 'Medialis' muscle (quadrate origin)	0	Absent			
	1	Present			
30. 'Medialis' muscle (insertion at mouth corner)	0	Present			
	1	Absent			
31. 'Profundus' muscle	0	Simple			
	1	Divided into anterior & posterior portions			
32. Levator pterygoidei origin	0	Confined to parietal			
	1	Part origin from post-orbital			
33. Protractor pterygoidei, Retractor vomeris and Retractor pterygoidei origins	0	Spread			
	1	Compact-arising from 'pinched' area			
34. Cutaneous muscle in head region	0	Thin			
	1	Thick			
35. Quadrato-maxillary ligament	0	Narrow anteriorly			
	1	Broad anteriorly			
36. Geniohyoideus muscle	0	Extends onto and anterior to lingual process of hyoid			
	1	Not extending onto hyoid lingual process			

Table 5. *cont.*

Summary of character states included in matrix			Additive binary codings (where relevant)		
37. Int. mand. post. muscle	0	Not attaching to hyoid lingual process			
	1	Attaching onto hyoid lingual process			
38. Transversus branchialis muscle	0	Not attaching to hyoid lingual process			
	1	Attaching onto hyoid lingual process			
39. Genioglossus muscle	0	With both lateral and medial heads			
	1	With lateral head only			
40. 'Geniomucosalis' muscle	0	Absent			
	1	Present			
			41·1	41·2	
41. Dentary dorsal and ventral extensions	0	Dorsal > Ventral	0	0	
	1	Dorsal = Ventral	1	0	
	2	Dorsal < Ventral	1	1	
42. Parietal and frontal bones	0	Separate beneath optic fenestra			
	1	Meet beneath optic fenestra			
43. Parietal medial crest	0	Absent			
	1	Present			
44. Posterior vidian foramen	0	Exposed			
	1	Roofed-over			
			45·1	45·2	45·3
45. Anterior vidian foramen	0	In parietal or on basisphenoid/ parietal suture	0	0	0
	1	Within basisphenoid	1	0	0
	2	(Two)–one between basisphenoid & parietal; the other just inside the basisphenoid	0	1	0
	3	(Two)–both within the basisphenoid	1	0	1
			46·1	46·2	
46. Optic/opthalmic foramina	0	Single foramen	0	0	
	1	Incompletely separated foramina	1	0	
	2	Double foramina	1	1	
47. Subcaudals	0	Paired			
	1	Single			
48. Caudal haemapophyses	0	Not fusing distally			
	1	Fusing distally			
49. Palatine medial wing	0	Present			
	1	Absent			
50. Palatine lateral process	0	Present			
	1	Absent			
			51·1	51·2	51·3
51. Palatine/Pterygoid articulation	0	Simple	0	0	0
	1	Disjunct	1	0	0
	2	Saddle-joint	0	1	0
	3	Palatine strongly overlapping mesial and lateral faces of pterygoid	0	1	1
52. Pterygoid/Palatine dorsal overlap	0	Pterygoid not overlapping Palatine			
	1	Pterygoid overlapping Palatine			
53. Foramen in palatine bone (lateral process)	0	Present			
	1	Absent			
			54·1	54·2	
54. Maxilla anterior extension	0	Maxilla extends > Palatine	0	0	
	1	Maxilla extends = Palatine	1	0	
	2	Maxilla extends	1	1	

Table 5. *cont.*

Summary of character states included in matrix			Additive binary codings (where relevant)			
55. Postorbital bone	0	Present				
	1	Absent				
56. Parietal ridge and venom gland anchoring ligament	0	Absent				
	1	Present				
			57·1	57·2	57·3	57·4
57. Prefrontal-frontal articulation	0	Oblique	0	0	0	0
	1	Anterior and lateral (square)	1	0	0	0
	2	Anterior	0	1	0	0
	3	Lateral	0	0	1	0
	4	Anterior and lateral (round)	0	0	0	1
58. Palatine teeth number	0	5·5–23·49				
	1	0–5·49				
59. Pterygoid teeth number	0	6·5–27·49				
	1	0–6·49				
60. Anterior portion of skull	0	46·7–58·6%				
	1	38·7–46·6%				
61. Relative length of quadrate	0	21·0–52·9%				
	1	13·0–20·9%				
62. Relative length of compound	0	51·8–67·7%				
	1	67·8–91·7%				
63. Relative length of dentary	0	46·8–67·7%				
	1	25·8–46·7%				
			64·1	64·2		
64. Relative length of supratemporal	0	17·3–45·2%	0	0		
	1	45·3–59·3%	1	0		
	2	3·3–17·2%	0	1		
65. Palatal pocket	0	Absent				
	1	Present				

scale (character 1·1) is absent in some individuals also a vestigial left lung (character 14) is variably present. A possible explanation is that such characters may have been variable in ancestral *Laticauda*, became relatively fixed in *semifasciata* and *laticaudata* lineages but remain variable in *L. colubrina*; a similar scenario is postulated by Arnold (1981: 19).

In conclusion, *L. colubrina* appears to be, in some ways, transitional between the *L. laticaudata* lineage and the divergent *L. semifasciata* lineage and cannot be unequivocally associated with either group on the basis of a phylogenetic analysis of its morphological characters. Biochemical evidence seems consistent with this conclusion. In terms of albumin immunological distance (Cadle & Gorman, 1981; Mao *et al.*, 1983), *L. semifasciata* appears rather divergent although, in tests with antisera to *L. semifasciata, L. colubrina* emerges as slightly closer to *L. semifasciata* than is *L. laticaudata*.

With regard to karyology, Gorman (1981) finds that *L. colubrina* has a diploid count of 34 which he believes corresponds with the primitive elapid condition; *L. laticaudata* and *L. semifasciata* have higher counts (40 and 38 respectively) and these are assumed to have evolved via centric fissions.

Kharin (1984) has recently suggested that *L. semifasciata* and *L. schistorhynchus* are sufficiently different from other *Laticauda* species to warrant being placed in a separate genus *(Pseudolaticauda)*. The above evidence demonstrates that while the *L. semifasciata* lineage is

Table 6.

Polarity patterns

A. $0 \longrightarrow 1$

Characters with pattern A:-
1·1,1·2,2,3,4,9,10,13,14,15,18,19,20,24,27,29,30,31,32,33,34,35,36,37,38,39,40,42,43,44,47,48,49,50,52,53,55,56,58,59,60,61,62,63,65.

B. $0 \longrightarrow 1 \longrightarrow 2$

Characters with pattern B:-
7,11,12,16,17,23,28,41,46,54.

C. $0 \longrightarrow 1 \longrightarrow 2 \longrightarrow 3$

Character with pattern C:-
26.

D. $1 \longleftarrow 0 \longrightarrow 2$

Characters with pattern D:-
5,6,8,21,25,64.

E. $1 \longleftarrow 0 \longrightarrow 2 \longrightarrow 3$

Character with pattern E:-
51.

F. $3 \longleftarrow 1 \longleftarrow 0 \longrightarrow 2$

Character with pattern F:-
45.

G.
$$\begin{tikzcd} 2 & & 3 \\ & 0 \arrow[ul] \arrow[ur] \arrow[dl] \arrow[dr] & \\ 1 & & 4 \end{tikzcd}$$

Character with pattern G:-
57.

indeed divergent from the other *Laticauda* lineages it appears possible that *L. colubrina* is phylogenetically closer to *L. semifasciata* than it is to *L. laticaudata*, a relationship that would be obscured if *L. colubrina* and *L. semifasciata* were placed in different genera. It is therefore thought best to here retain the genus *Laticauda* in its former broad sense.

Wider relationships of genus *Laticauda*

Phenetic analysis

Simple matching coefficients and unweighted pair group clustering were used to depict phenetic relationships between all the elapids in the sample (Table 8 and Fig. 4).

Laticauda and other sea snakes appear to share only a relatively low level of phenetic similarity (see also Voris, 1977: 91). Additionally *Laticauda* shares more overall similarity with the terrestrial elapines in the sample than with the hydrophine sea snakes.

Phylogenetic analyses

Wagner Parsimony

The program used in the present study is Farris' 'Advancement sequenced Wagner Program phase AF, version 1/4/69'. The data matrix (Table 7) is modified for Wagner analysis to the extent that variable states are treated as derived (state 1) and unrecordable states are scored as primitive (0). The order of input in Farris' algorithm is governed by advancement-indices; taxa with the smallest number of derived characters being incorporated first, those with the greatest

The numbers in subsequent figures and tables refer to the following taxa:

1 *Laticauda laticaudata*
2 *Laticauda crockeri*
3 *Laticauda colubrina*
4 *Laticauda semifasciata*
5 *Laticauda schistorhynchus*
6 *Parapistocalamus hedigeri*
7 *Calliophis macclellandii*
8 *Calliophis japonicus*
9 *Maticora bivirgata*
10 *Micrurus surinamensis*
11 *Micrurus lemniscatus*
12 *Micrurus psyches*
13 *Ephalophis greyi*
14 *Aipysurus fuscus*
15 *Bungarus flaviceps*

Table 7. Character state matrix
The species are represented by the identification numbers given in caption to Fig. 4. Where a derived state is only variably present, this is indicated by 'V'; where data are missing or otherwise unrecordable '–' is used. Character state numbers preceded by '–' indicates those states for which polarity assessments are rather arbitrary.

	Character nos.																		
	1·1	1·2	2	3	4	5·1	5·2	6·1	6·2	7·1	7·2	8·1	8·2	9	10	11·1	11·2	–12·1	12·2
1	0	0	0	0	0	0	0	0	0	1	1	0	0	1	1	0	0	1	0
2	0	0	0	0	0	0	0	0	0	1	1	0	0	1	1	0	0	1	0
3	V	0	0	0	0	0	0	0	1	1	1	0	1	1	1	1	1	1	1
4	1	0	1	0	0	0	0	0	0	1	0	0	1	1	1	0	0	0	0
5	1	0	1	0	0	0	0	0	0	1	0	0	1	1	1	0	0	0	0
6	0	0	0	0	0	V	0	1	0	0	0	0	0	0	0	0	0	0	0
7	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0
8	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	1	1	1
10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
13	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	1	1	1	0
14	V	1	0	1	1	0	V	0	1	1	0	0	0	0	1	1	1	1	1
15	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	1

Table 7. *cont.*

	−13	14	15	16·1	16·2	−17·1	−17·2	−18	−19	−20	−21·1	−21·2	−23·1	−23·2	−24	25·1	25·2	26·1	26·2
1	0	0	0	1	0	1	0	1	1	0	0	0	1	0	1	0	1	1	1
2	1	0	0	1	0	1	0	1	1	0	0	0	1	V	1	0	1	1	1
3	0	V	1	1	0	1	0	0	1	0	0	0	0	0	1	0	1	1	1
4	1	1	1	1	0	1	0	0	1	0	1	0	1	0	1	0	1	1	1
5	1	1	1	1	0	1	0	0	1	0	1	0	1	0	1	0	1	1	1
6	1	1	0	0	0	1	0	0	0	1	0	0	1	0	1	0	1	1	1
7	0	1	0	0	0	1	1	0	0	1	0	1	0	0	0	0	0	0	0
8	0	1	1	0	0	1	0	0	0	1	0	1	1	1	1	0	0	0	0
9	1	1	0	0	0	1	0	0	0	1	0	0	1	0	1	1	0	–	–
10	0	1	0	0	0	1	0	0	0	1	0	1	0	0	0	0	1	1	1
11	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	1	1	1
12	0	1	0	0	0	1	0	0	0	1	0	1	0	0	0	0	1	0	0
13	1	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1
14	1	1	1	1	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0
15	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0

	26·3	27	28·1	28·2	−29	−30	−31	−32	33	34	35	36	37	38	39	40	41·1	41·2	42
1	0	1	0	0	1	0	0	1	0	0	0	1	1	1	0	0	1	1	V
2	0	1	0	0	1	0	0	1	0	0	0	1	1	1	0	0	1	1	0
3	0	1	0	0	1	0	0	1	0	0	0	1	1	1	0	0	1	1	0
4	1	1	0	0	0	1	0	0	1	1	1	1	1	1	0	0	1	1	0
5	1	1	0	0	0	1	0	0	1	1	1	1	1	1	0	0	1	1	0
6	0	1	1	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1
7	0	1	0	0	0	1	1	–	0	0	0	0	0	0	0	0	1	1	0
8	0	1	0	0	1	1	1	–	0	0	0	0	0	0	0	0	0	0	0
9	–	–	–	–	0	1	1	0	0	0	0	0	0	0	0	0	1	1	0
10	0	1	0	0	1	0	0	–	0	0	0	0	0	0	0	0	1	1	0
11	0	1	1	1	1	1	0	–	0	0	0	0	0	0	0	0	1	1	0
12	0	1	1	0	1	0	0	–	0	0	0	0	0	0	0	0	1	1	0
13	1	1	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0
14	0	1	0	0	0	0	0	0	0	0	1	1	1	1	0	1	0	0	1
15	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0

	–43	44	45·1	45·2	45·3	46·1	46·2	47	48	49	50	51·1	51·2	51	52	53	54·1	54·2	55
1	1	0	0	0	0	1	1	0	V	1	0	0	1	0	0	V	0	0	0
2	1	V	0	0	0	1	1	0	V	1	0	0	1	0	0	0	0	0	0
3	1	0	0	0	0	1	1	0	V	1	0	0	1	0	0	0	0	0	0
4	1	V	0	0	0	1	1	0	V	1	0	0	1	0	0	0	0	0	0
5	1	0	0	0	0	1	0	0	V	1	0	0	1	0	0	0	0	0	0
6	0	0	1	0	1	0	0	0	0	0	1	0	1	1	1	–	0	0	0
7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8	1	V	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
9	1	0	0	0	0	1	1	0	0	0	1	0	0	0	0	–	0	0	0
10	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1
11	1	0	1	0	0	1	1	0	0	0	0	1	0	0	0	1	0	0	1
12	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1
13	1	1	0	0	0	0	0	1	1	1	1	0	1	1	1	–	1	1	0
14	0	V	0	1	0	1	1	1	1	1	1	0	1	0	0	–	0	0	0
15	1	1	1	0	0	1	1	V	0	0	0	0	0	0	1	0	1	1	0

	56	57·1	57·2	57·3	–58	59	–60	–61	–62	–63	–64·1	–64·2	65
1	1	0	1	0	1	0	V	0	1	1	0	V	1
2	1	0	1	0	1	0	0	0	1	1	0	0	1
3	1	0	1	0	V	0	1	0	1	1	0	V	1
4	0	1	0	0	0	0	0	0	1	1	0	0	1
5	0	1	0	0	0	0	0	0	1	1	0	0	1
6	0	0	0	0	0	0	0	1	0	1	1	0	0
7	1	0	1	0	0	1	0	1	0	1	0	0	0
8	1	0	1	0	0	0	1	0	0	1	1	0	0
9	1	0	1	0	0	1	0	1	1	1	0	0	0
10	1	0	1	0	0	0	0	0	1	1	0	0	0
11	1	0	1	0	0	1	0	0	1	1	0	0	0
12	1	0	1	0	0	1	0	1	1	1	0	0	0
13	1	0	0	1	0	0	1	0	0	0	0	0	0
14	1	0	0	1	0	0	0	0	0	1	0	0	0
15	1	1	0	0	0	0	0	0	0	0	0	0	0

Table 8. Overall similarity matrix (simple matching coefficients).

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
15	573	584	573	567	551	602	722	693	726	676	688	676	665	534
14	528	540	597	534	523	489	534	523	530	500	466	500	665	
13	511	528	540	511	517	540	563	603	549	575	540	529		
12	642	631	597	511	528	707	841	756	753	932	898			
11	676	665	631	591	585	695	761	722	753	920				
10	688	676	642	580	597	730	795	778	716					
9	598	616	604	561	555	701	827	710						
8	591	597	568	534	545	632	801							
7	585	585	551	511	528	695								
6	563	568	489	574	591									
5	725	747	725	978										
4	730	758	730											
3	865	848												
2	949													

Taxa are represented by the identification numbers given in caption to Fig. 4.

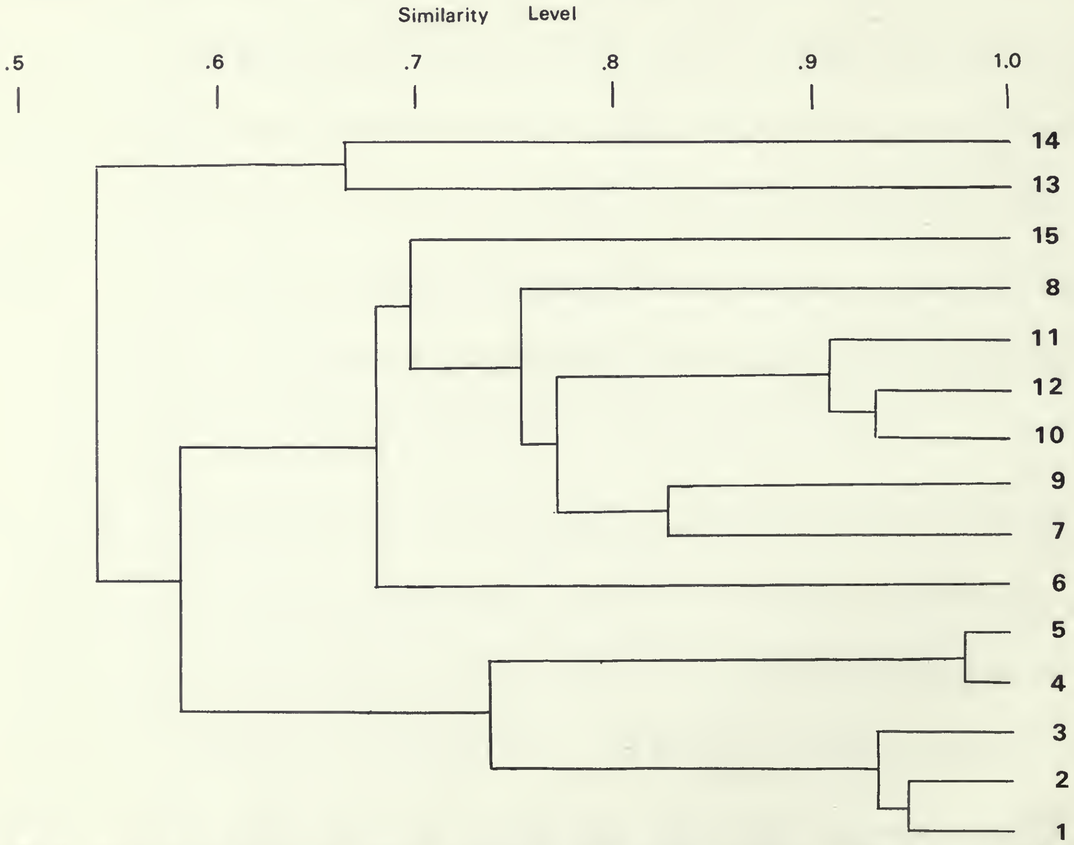

Fig. 4 Dendrogram based on overall similarity (using simple matching coefficients and the unweighted pair group method of clustering). Numbers indicate the following taxa: 1 *Laticauda laticaudata;* 2 *Laticauda crockeri;* 3 *Laticauda colubrina;* 4 *Laticauda semifasciata;* 5 *Laticauda schistorhynchus;* 6 *Parapistocalamus hedigeri;* 7 *Calliophis macclellandii;* 8 *Calliophis japonicus;* 9 *Maticora bivirgata;* 10 *Micrurus surinamensis;* 11 *Micrurus lemniscatus;* 12 *Micrurus psyches;* 13 *Ephalophis greyi;* 14 *Aipysurus fuscus;* 15 *Bungarus flaviceps.*
The cophenetic correlation coefficient of this dendrogram is 0·9425.

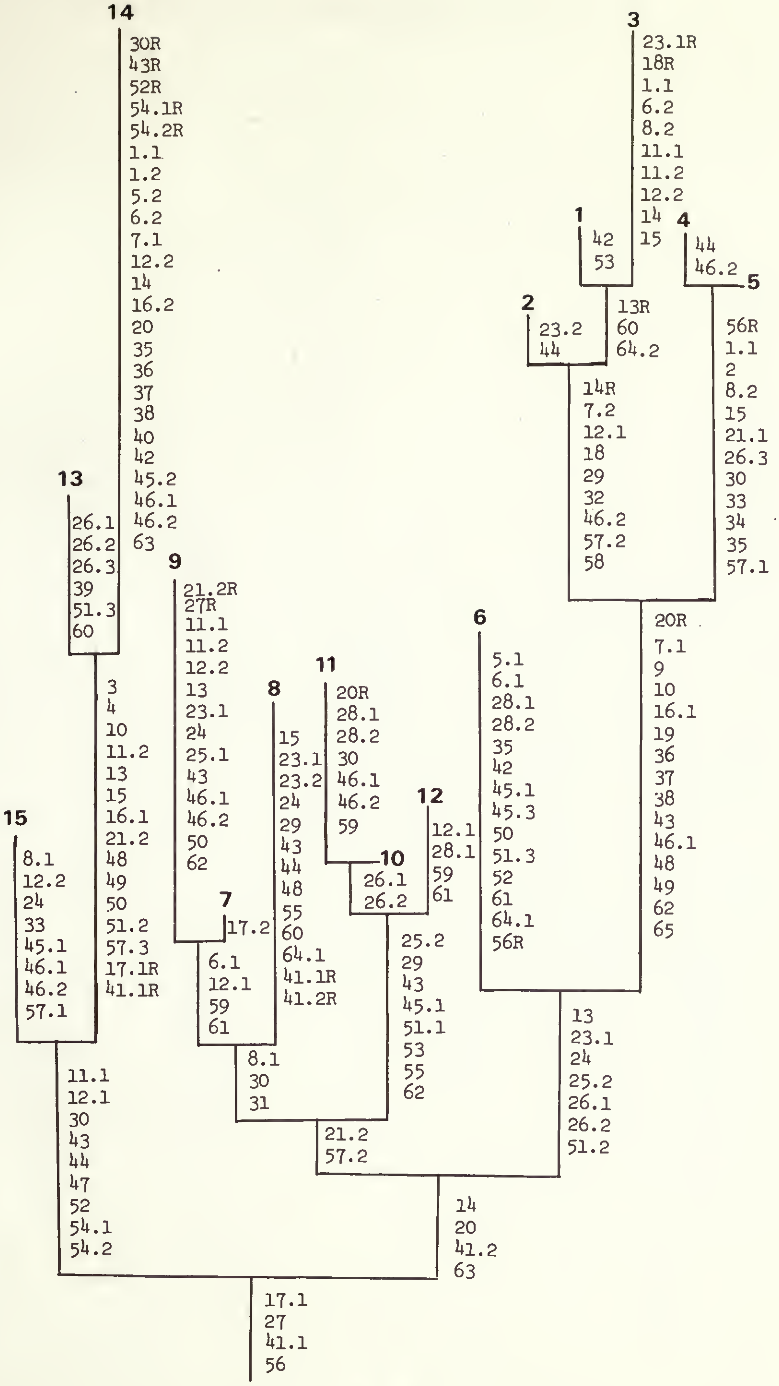
14
30R 43R 52R 54.1R 54.2R 1.1 1.2 5.2 6.2 7.1 12.2 14 16.2 20 35 36 37 38 40 42 45.2 46.1 46.2 63
13
26.1 26.2 26.3 39 51.3 60
3 4 10 11.2 13 15 16.1 21.2 48 49 50 51.2 57.3 17.1R 41.1R
15
8.1 12.2 24 33 45.1 46.1 46.2 57.1
11.1 12.1 30 43 44 47 52 54.1 54.2
9
21.2R 27R 11.1 11.2 12.2 13 23.1 24 25.1 43 46.1 46.2 50 62
7
17.2
6.1 12.1 59 61
8
15 23.1 23.2 24 29 43 44 48 55 60 64.1 41.1R 41.2R
8.1 30 31
11
20R 28.1 28.2 30 46.1 46.2 59
10
26.1 26.2
12
12.1 28.1 59 61
25.2 29 43 45.1 51.1 53 55 62
21.2 57.2
6
5.1 6.1 28.1 28.2 35 42 45.1 45.3 50 51.3 52 61 64.1 56R
3
23.1R 18R 1.1 6.2 8.2 11.1 11.2 12.2 14 15
1
42 53
4
44 46.2
5
2
23.2 44
13R 60 64.2
14R 7.2 12.1 18 29 32 46.2 57.2 58
56R 1.1 2 8.2 15 21.1 26.3 30 33 34 35 57.1
20R 7.1 9 10 16.1 19 36 37 38 43 46.1 48 49 62 65
13 23.1 24 25.2 26.1 26.2 51.2
14 20 41.2 63
17.1 27 41.1 56

Fig. 5a

Fig. 5 Wagner tree runs. Taxon numbers as in Fig. 4. Character state transformations marked along branches; 'R' following a character number indicates that a reversal has been hypothesized. **(a)** Run 1; entire data set, advancement-index sequenced. **(b)** Run 2; entire data set, taxa in order of Le Quesne test labelling. **(c)** Run 3; 'arbitrary' characters excluded, advancement-index sequenced. **(d)** Run 4; 'arbitrary' characters excluded; taxa in order of Le Quesne test labelling.

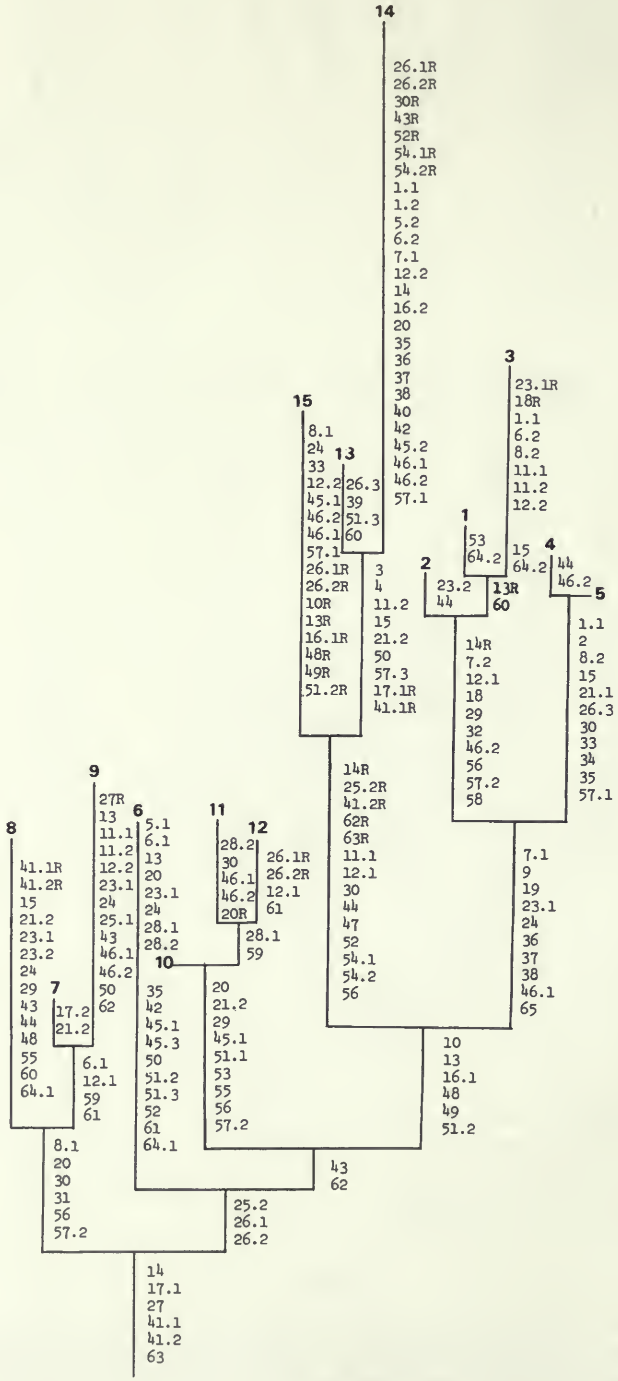
14
26.1R
26.2R
30R
43R
52R
54.1R
54.2R
1.1
1.2
5.2
6.2
7.1
12.2
14
16.2
20
35
36
37
38
40
42
45.2
46.1
46.2
57.1
15
8.1
24
33
12.2
45.1
46.2
46.1
57.1
26.1R
26.2R
10R
13R
16.1R
48R
49R
51.2R
13
26.3
39
51.3
60
3
4
11.2
15
21.2
50
57.3
17.1R
41.1R
3
23.1R
18R
1.1
6.2
8.2
11.1
11.2
12.2
1
53
64.2
15
64.2
13R
60
2
23.2
44
4
44
46.2
5
1.1
2
8.2
15
21.1
26.3
30
33
34
35
57.1
14R
7.2
12.1
18
29
32
46.2
56
57.2
58
7.1
9
19
23.1
24
36
37
38
46.1
65
14R
25.2R
41.2R
62R
63R
11.1
12.1
30
44
47
52
54.1
54.2
56
10
13
16.1
48
49
51.2
9
27R
13
11.1
11.2
12.2
23.1
24
25.1
43
46.1
46.2
50
62
6
5.1
6.1
13
20
23.1
24
28.1
28.2
11
28.2
30
46.1
46.2
20R
12
26.1R
26.2R
12.1
61
28.1
59
10
35
42
45.1
45.3
50
51.2
51.3
52
61
64.1
20
21.2
29
45.1
51.1
53
55
56
57.2
8
41.1R
41.2R
15
21.2
23.1
23.2
24
29
43
44
48
55
60
64.1
7
17.2
21.2
6.1
12.1
59
61
8.1
20
30
31
56
57.2
43
62
25.2
26.1
26.2
14
17.1
27
41.1
41.2
63

Fig. 5b

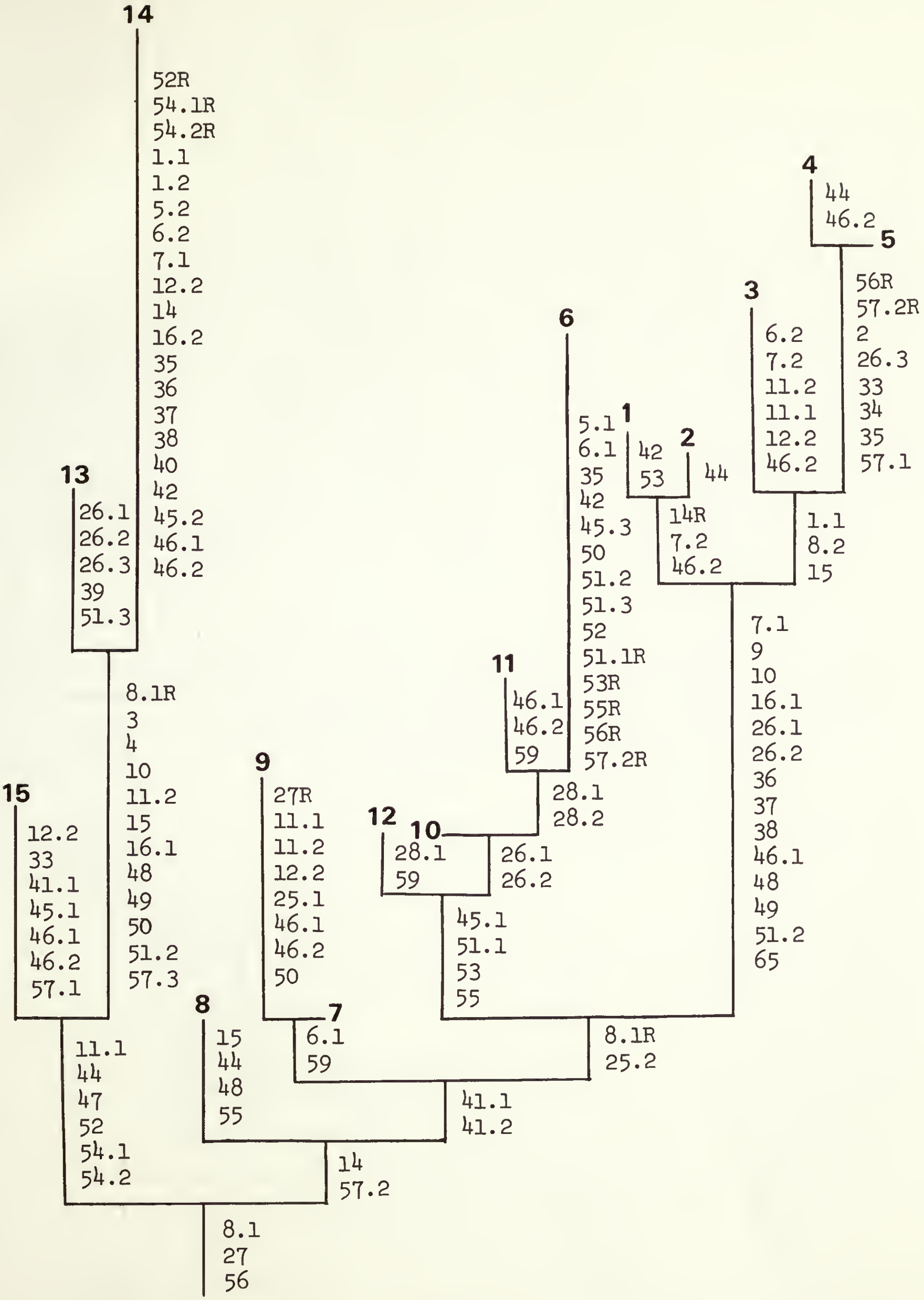
14
52R
54.1R
54.2R
1.1
1.2
5.2
6.2
7.1
12.2
14
16.2
35
36
37
38
40
42
45.2
46.1
46.2
13
26.1
26.2
26.3
39
51.3
8.1R
3
4
10
11.2
15
16.1
48
49
50
51.2
57.3
15
12.2
33
41.1
45.1
46.1
46.2
57.1
11.1
44
47
52
54.1
54.2
8
15
44
48
55
9
27R
11.1
11.2
12.2
25.1
46.1
46.2
50
7
6.1
59
41.1
41.2
14
57.2
8.1
27
56
12
28.1
59
10
26.1
26.2
45.1
51.1
53
55
8.1R
25.2
11
46.1
46.2
59
28.1
28.2
6
5.1
6.1
35
42
45.3
50
51.2
51.3
52
51.1R
53R
55R
56R
57.2R
1
42
53
2
44
14R
7.2
46.2
3
6.2
7.2
11.2
11.1
12.2
46.2
4
44
46.2
5
56R
57.2R
2
26.3
33
34
35
57.1
1.1
8.2
15
7.1
9
10
16.1
26.1
26.2
36
37
38
46.1
48
49
51.2
65

Fig. 5c

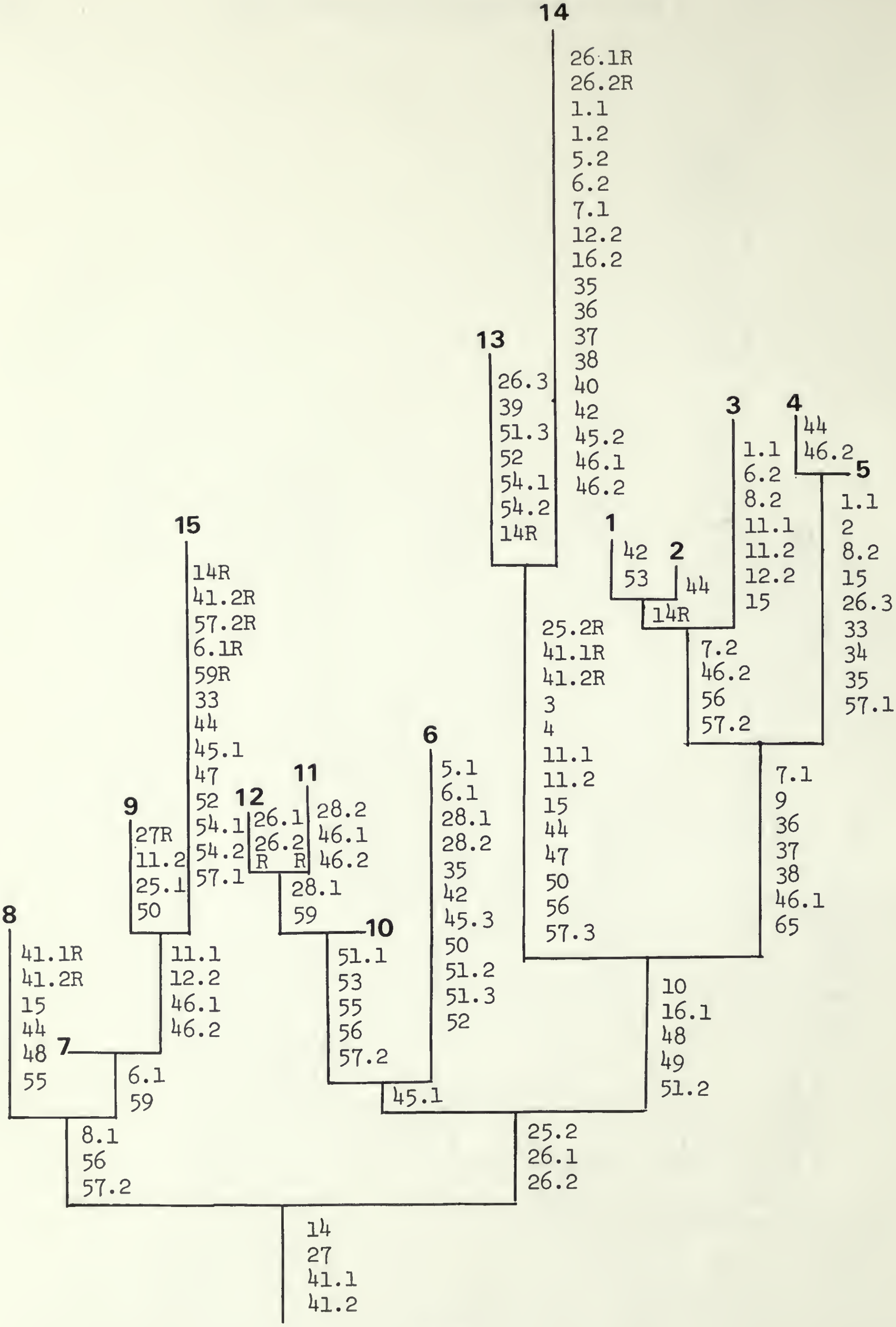
14
26.1R
26.2R
1.1
1.2
5.2
6.2
7.1
12.2
16.2
35
36
37
38
40
42
45.2
46.1
46.2
13
26.3
39
51.3
52
54.1
54.2
14R
3
1.1
6.2
8.2
11.1
11.2
12.2
15
4
44
46.2
5
1.1
2
8.2
15
26.3
33
34
35
57.1
1
42
53
2
44
14R
7.2
46.2
56
57.2
25.2R
41.1R
41.2R
3
4
11.1
11.2
15
44
47
50
56
57.3
7.1
9
36
37
38
46.1
65
15
14R
41.2R
57.2R
6.1R
59R
33
44
45.1
47
52
54.1
54.2
57.1
9
27R
11.2
25.1
50
12
26.1 R
26.2 R
11
28.2
46.1
46.2
28.1
59
10
51.1
53
55
56
57.2
6
5.1
6.1
28.1
28.2
35
42
45.3
50
51.2
51.3
52
45.1
10
16.1
48
49
51.2
8
41.1R
41.2R
15
44
48
55
7
11.1
12.2
46.1
46.2
6.1
59
8.1
56
57.2
25.2
26.1
26.2
14
27
41.1
41.2

Fig. 5d

number of derived characters are added last. However Felsenstein (1981) recommends performing a number of runs, altering the order of input of taxa, as a trial & error strategy for finding the shortest tree.

In all four runs were undertaken:

1. Entire data set; advancement-index sequenced.
2. Entire data set; taxa in order of Le Quesne test labelling (see p. 156).
3. Characters with more arbitrarily scored polarities excluded; advancement-index sequenced.
4. Characters with more arbitrarily scored polarities excluded; Le Quesne test labelling governing the order of input of taxa (see p. 156).

With the full data set, examined by the unmodified sequence method (run 1), *Laticauda* and the true sea snakes appear not especially closely related; *Parapistocalamus* is sister to *Laticauda* (Fig. 5a). Altering the program to treat taxa in a modified order based on Le Quesne test labelling (run 2) produced a less parsimonious tree (213 steps vs. 204 steps). The topology of this tree (Fig. 5b) suggests that *Laticauda*, 'true' sea snakes and kraits *(Bungarus)* are all relatively closely related. Reducing the data set to consider only the more confidently scored characters (runs 3 and 4) produced two more topologies for consideration. In the advancement sequenced run (3) Fig. 5c, the tree was similar to that produced in run 1 in the sense that *Laticauda* and the true sea snakes appear only remotely related. However, run 3 estimates the sister of *Laticauda* to be not only *Parapistocalamus* but also *Micrurus*. Repeating the run, this time with Le Quesne test sequencing (run 4) Fig. 5d produced an equally parsimonious tree (the trees produced by both runs 3 and 4 are 139 steps). However, the topology of the tree resulting from run 4 resembles that of rejected run 2 in closely relating *Laticauda* and the 'true' sea snakes with each other, *Bungarus* is not considered close to the sea snakes though, instead *Parapistocalamus* and *Micrurus* together form the sea snake sister group.

Detection of homoplasies in Wagner trees

(i) Procedural estimate

The general amount of homoplasy (reversals and parallels) present in Wagner trees may be estimated by dividing the number of derived character states by the total number of character state changes (steps) in the tree. The result, expressed as a percentage, is termed the consistency ratio or homoplasy index. The homoplasy indices of various Wagner tree runs in the present study are as follows:

		Homoplasy Index
Run 1	89/204 × 100	43·63%
Run 2	89/213 × 100	41·78%
Runs 3 & 4	65/139 × 100	46·76%

In comparison, Kluge (1976: 45) derived a scheme for pygopodid lizards that has rather less 'noise' than is detected in the present study (its homoplasy index is 57·2%) whereas Moody's (1980: 124) Wagner tree for agamid lizards has almost twice as much homoplasy as the trees in the present study (the index is 24·7%).

The Wagner tree algorithm, by creating hypothetical intermediates at nodes, assesses the implications of each topology for every character state so that the number of reversals and parallels hypothesized for each character may be compared. Table 9 shows the changes of each character implicit in Wagner trees produced by runs 1, 3 and 4. However the Wagner tree algorithm gives a purely procedural estimate of homoplasies; some of the decisions, when judged by biological criteria, may appear unrealistic. For example, character 14 (vestigial left lung loss) is hypothesized to have been reversed three times in runs 3 and 4 but, biologically, a more likely explanation may be that such a vestige would have instead been lost, in parallel, on several occasions.

(ii) 'Fours' analysis

Underwood (1982) recently suggested a method for detecting parallelism. This program enables taxa to be selected in groups of four and gives the distribution of derived states among these taxa; in this way conflicts of evidence are clearly exposed.

Table 9. Number of parallels (P) & reversals (R) hypothesized for some Wagner tree runs.

Character	Run 4	Run 3	Run 1	Character	Run 4	Run 3	Run 1
1·1	2P	1P	2P	32	–	–	0
1·2	0	0	0	33	1P	1P	1P
2	0	0	0	34	0	0	0
3	0	0	0	35	2P	2P	2P
4	0	0	0	36	1P	1P	1P
5·1	0	0	0	37	1P	1P	1P
5·2	0	0	0	38	1P	1P	1P
6·1	1R, 1P	1P	1P	39	0	0	0
6·2	1P	1P	1P	40	0	0	0
7·1	1P	1P	1P	41·1	2R	1P	2R
7·2	0	1P	0	41·2	3R	0	1R
8·1	0	2R	1P	42	2P	2P	2P
8·2	1P	0	1P	43	–	–	1R, 4P
9	0	0	0	44	4P	3P	3P
10	0	1P	1P	45·1	1P	1P	2P
11·1	2P	2P	2P	45·2	0	0	0
11·2	2P	2P	2P	45·3	0	0	0
12·1	–	–	3P	46·1	3P	4P	4P
12·2	2P	3P	3P	46·2	4P	6P	5P
13	–	–	1R, 2P	47	1P	0	0
14	3R	1R, 1P	1R, 2P	48	1P	2P	2P
15	3P	2P	3P	49	0	1P	1P
16·1	0	1P	1P	50	2P	2P	2P
16·2	0	0	0	51·1	0	1R	0
17·1	–	–	1R	51·2	1P	2P	1P
17·2	–	–	0	51·3	1P	1P	1P
18	–	–	1R	52	2P	1R, 1P	1R, 1P
19	–	–	0	53	1P	1R, 1P	1P
20	–	–	2R, 1P	54·1	1P	1R	1R
21·1	–	–	0	54·2	1P	1R	1R
21·2	–	–	1R, 1P	55	1P	1R, 1P	1P
23·1	–	–	1R, 2P	56	3P	2R	2R
23·2	–	–	1P	57·1	1P	1P	1P
24	–	–	3P	57·2	1R, 2P	2R	1P
25·1	0	0	0	57·3	0	0	0
25·2	1R	0	1P	58	–	–	0
26·1	2R	2P	2P	59	1R, 1P	2P	2P
26·2	2R	2P	2P	60	–	–	2P
26·3	1P	1P	1P	61	–	–	2P
27	1R	1R	1R	62	–	–	2P
28·1	1P	1P	2P	63	–	–	1P
28·2	1P	0	1P	64·1	–	–	1P
29	–	–	2P	64·2	–	–	0
30	–	–	1R, 2P	65	0	0	0
31	–	–	0				

Seven species were selected to test the robustness of the various Wagner trees produced in the present study: *Laticauda crockeri, Laticauda semifasciata, Parapistocalamus hedigeri, Micrurus surinamensis, Ephalophis greyi, Aipysurus fuscus, Bungarus flaviceps.*

The topologies of these taxa in various Wagner tree runs are shown in Fig. 6. Table 10 gives an indication of the character states supporting various combinations of the seven species. Table

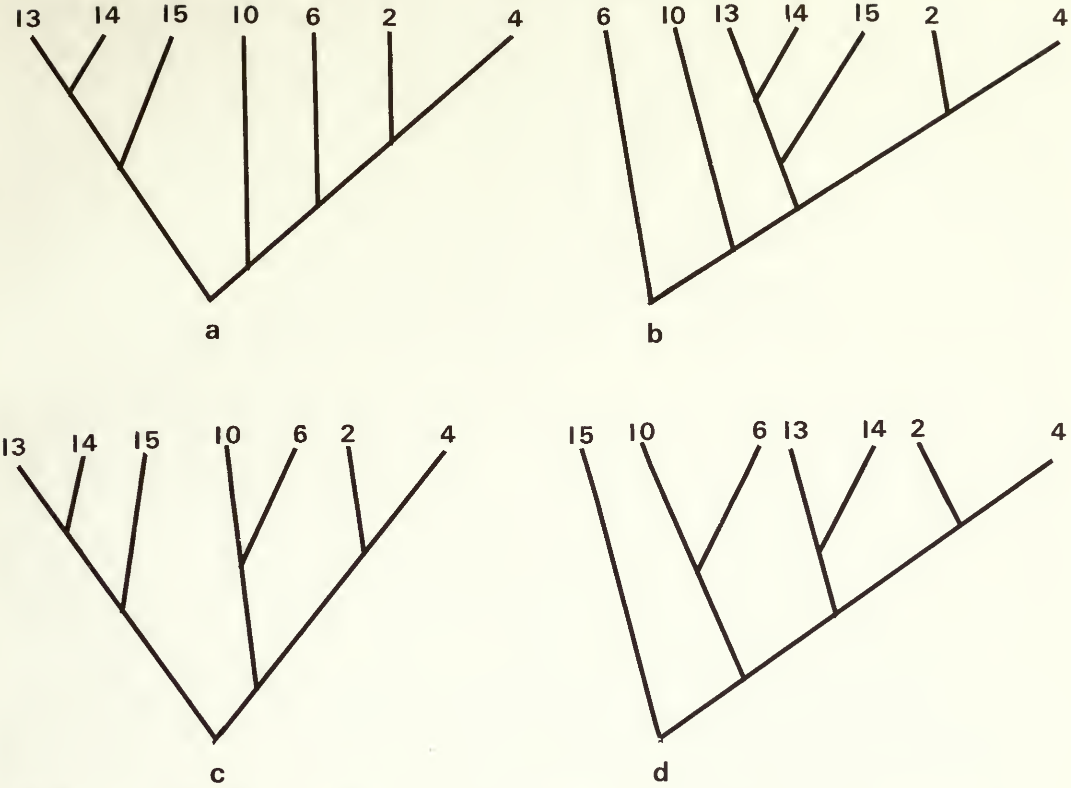

Fig. 6 'Fours' analysis. Topologies, in various Wagner tree runs, of seven taxa selected for 'fours' analysis. Taxa numbered as in Fig. 4. (a) Wagner tree run 1. (b) Wagner tree run 2. (c) Wagner tree run 3. (d) Wagner tree run 4.

10(a) deals with *Micrurus surinamensis* (10), *Parapistocalamus hedigeri* (6), *Laticauda crockeri* (2) and *Laticauda semifasciata* (4). Wagner run 1 suggests an asymmetric dichotomy pattern for these taxa whereas run 3 suggests symmetric dichotomies. Of the non-arbitrary characters supporting the alternatives there is a tie; one character 51·2 (saddle-joint between palatine and pterygoid) supporting run 1 while character 45·1 (position of the anterior vidian foramen) supports run 3. Three non-arbitrary characters are incompatible with either of these arrangements: 56 (parietal ridge) and 57·2 (prefrontal/frontal articulation) associate *Micrurus surinamensis* (10) and *Laticauda crockeri* (2), while 14 (absence of a vestigial left lung) occurs in *Micrurus* (10), *Parapistocalamus* (6) and *Laticauda semifasciata* (4). However the small number of characters suggesting that *L. crockeri* and *L. semifasciata* might have closer affinities with taxa outside the genus are outweighed by thirteen non-arbitrary derived characters shared by these two species of *Laticauda*.

Another fours print-out (Table 10b), this time replacing *Parapistocalamus* with *Aipysurus fuscus* (14) brings into consideration some of the characters supporting the affinities of *Laticauda* with other sea snakes. The proposition that *Micrurus surinamensis* (10) is more closely related to *Laticauda* (4) than is *Aipysurus* (14) (runs 1 and 3) is supported by five non-arbitrary characters but out-voted by twelve non-arbitrary characters supporting the close affinity of *Laticauda* with *Aipysurus*. Additionally, the assumption that *L. crockeri* is closely related to *L. semifasciata* (supported by characters 9 and 65) is challenged by three characters (1·1, 15 and 35) which suggest that *L. semifasciata* is more closely related to *Aipysurus*, a topology not suggested by any of the Wagner runs in the present study.

Table 10. ‘Fours’ analysis.

(*a*) Taxon numbers 10 6 2 4:-
1100: –20 45·1
0011: 7·1 9 10 16·1 –19 36 37 38 44 46·1 46·2 48 49 65
1010: –29 56 57·2
0101: 35
1101: 14
0111: 51·2
1000: 51·1 55
0100: 5·1 6·1 28·1 28·2 42 45·3 50 51·3 52
0010: 7·2
0001: 1·1 2 8·2 15 26·3 33 34 57·1

(*b*) Taxon numbers 10 2 4 14:-
1100: –29 57·2
0011: 1·1 15 35
0101: –12·1
1001: –20 –21·2
0110: 9 –19 –23·1 –24 65
1110: 25·2 26·1 26·2 41·1 41·2
1101: 56
1011: 14
0111: 7·1 10 16·1 36 37 38 44 46·1 46·2 48 49 51·2
1000: 45·1 51·1 55
0100: 7·2
0010: 2 8·2 26·3 33 34 57·1
0001: 1·2 3 4 5·2 6·2 11·1 11·2 12·2 16·2 40 42 45·2 47 50 57·3

(*c*) Taxon numbers 10 13 4 14:-
0011: 1·1 7·1 35 36 37 38 46·1 46·2
1010: –17·1 25·2 41·1 41·2 –62
0101: 3 4 11·1 11·2 –12·1 47 50 57·3
1001: –20
0110: 26·3 –30
1110: 26·1 26·2
1101: 56
1011: 14
0111: 10 15 16·1 44 48 49 51·2
1000: 45·1 51·1 55 57·2
0100: 39 51·3 52 54·1 54·2
0010: 2 8·2 9 33 34 57·1 65
0001: 1·2 5·2 6·2 12·2 16·2 40 42 45·2

(*d*) Taxon numbers 10 15 4 14:-
1100: 45·1
0011: 1·1 7·1 10 –13 15 16·1 35 36 37 38 48 49 51·2
1010: 25·2 26·1 26·2 41·2 –62
0101: 11·1 –12·1 12·2 47
1001: –20 –21·2
0110: –24 –30 33 57·1
1110: 41·1
1101: 56
1011: 14
0111: 44 46·1 46·2
1000: 51·1 55 57·2
0100: 8·1 52 54·1 54·2
0010: 2 8·2 9 26·3 34 65
0001: 1·2 3 4 5·2 6·2 11·2 16·2 40 42 45·2 50 57·3

Character state numbers preceded by ‘–’ are those for which polarity assessments are rather arbitrary. Arbitrary states are only given when these are shared between taxa.

Introducing another hydrophiine sea snake into the fours analysis and withdrawing *Laticauda crockeri* leads to the print-out given in Table 10 (c). Seven non-arbitrary characters support the inclusion of *Laticauda semifasciata* (4) in the same group as *Aipysurus* (14) and *Ephalophis* (13) whereas only three suggest that *L. semifasciata* is more closely related to *Micrurus surinamensis* (10) than it is to hydrophiine sea snakes. Relationships within the sea snakes are balanced between the seven non-arbitrary characters supporting the affinities of *Aipysurus* with *Ephalophis* and the eight non-arbitrary characters supporting the association of *Aipysurus* with *L. semifasciata.*

As *L. semifasciata* and *Aipysurus fuscus* are the respective laticaudines and hydrophiines that seem to have most derived characters in common, a fourth print-out (Table 10d) was obtained to assist in evaluating the evidence supporting laticaudine/hydrophiine relationships. In addition to *L. semifasciata* (4) and *A. fuscus* (14) the elapines *Bungarus flaviceps* (15) (a species which is associated with hydrophiine sea snakes in Wagner tree runs 1–3) and *Micrurus surinamensis* (10) are also included.

If it be assumed that *Laticauda* and hydrophiine sea snakes do not share close common ancestry it might be anticipated that the majority of derived features shared by the two groups would be parallel marine adaptations. However, of the twelve non-arbitrary derived states shared by *Laticauda semifasciata* and *Aipysurus fuscus,* only three appear to be likely aquatic adaptations, namely: 10 (paddle-shaped tail), 15 (tracheal lung present), 16 (muscular air sac). Of the other characters, 1·1 (azygous prefrontal) and 7·1 (marginal lower lip scales) are possibly not homologous in the two groups. *Aipysurus fuscus* is inclined to have its head shields irregularly fragmented therefore the inference that these are truly derived characters, shared by *Aipysurus* and *Laticauda*, may in fact be spurious. Absence of a palatine medial wing (49) and presence of a saddle-joint between palatine and pterygoid (51) are both found in a number of other taxa (Marx & Rabb, 1972 and McCarthy, 1982), and appear likely to have occurred independently several times in snake evolution. Broad flaring of the quadrato-maxillary ligament (35) has been found additionally in *Parapistocalamus.* The unusual hyoid muscle conditions in *Laticauda* and *Aipysurus* (characters 36, 37 and 38) do appear to be restricted to these two genera and may be potentially robust indicators of phyletic affinity but the extent of the distribution of these characters remains to be more fully investigated (McCarthy, in prep.). Character 48 (caudal haemapophyses fused) is unusual for snakes and might be a significant similarity shared between *Laticauda, Aipysurus, Emydocephalus,* and *Ephalophis;* the only elapines in which this state has been found are two species of *Calliophis* (McCarthy, 1982: 146).

Characters shared by *Laticauda semifasciata* and *Micrurus surinamensis* are:- venom gland down-turning (25·2), quadrate attachment of the superficialis muscle (26·1, 26·2) and a small dorsal extension of the dentary in comparison with the ventral extension (41·2). None of these characters are exclusively shared by *Laticauda* and *Micrurus* but at least 25·2 and 41·2 are rather restricted in their distributions among other elapids (McCarthy, 1982: 101 and 132). Characters 26·1 and 26·2 have rather wider distributions, occurring for example in a number of Australasian elapines (McDowell, 1967: 536 ff.).

Compatibility

In contrast to parsimony methods, which aim to find the shortest tree thereby minimizing assumptions of homoplasy, compatibility methods exist to find a tree which is compatible with the largest number of characters irrespective of the number of changes that may need to be assumed in other characters (Felsenstein, 1982). When pairs of binary characters are compared and all four possible combinations of states are found it is a logical consequence that at least one of the character states is not uniquely derived (Le Quesne, 1969).

The program used in the present study is that devised by Underwood, which compiles a character-pair matrix, works out the number of Le Quesne test incompatibilities per character and then computes the ratio between actual and expected failure rates. Additionally the number of times the occurrence of a character state in a particular species is uniquely responsible for Le Quesne test incompatibility is noted; this procedure is termed 'labelling' by Guise, Peacock & Gleaves (1982). The number of labelling events for each species is totalled (Table 11) and the

Table 11. Le Quesne test; the number of labelling events per taxon.

Taxon	Number of times labelled
1	86
2	50
3	156
4	10
5	6
6	125
7	19
8	85
9	56
10	17
11	37
12	19
13	98
14	203
15	111

results used to decide the order of input of taxa in some Wagner parsimony test runs (p. 151). This procedure for input of taxa may be desirable because initial construction of the Wagner tree can be accomplished using taxa with the fewest incompatibilities. 'Problem' taxa are later added to a relatively robust structure rather than being allowed to influence the topology of that structure at an early stage.

The Le Quesne test failure rates of the characters are shown in Table 12. An observed: expected ratio of 0·5 indicates those characters that have survived the test twice as well as could have been anticipated on a null hypothesis of random distribution of states of the characters (Le Quesne, 1972). Fourteen characters having a ratio of 0·5 or better are shown in Figure 7 together with the cladograms described by them. Ten of the fourteen characters that best survive the test can be nested within a single cladogram (Fig. 7a). These ten states suggest relationships within *Laticauda*, the distinctiveness of the genus and also its possible relationships with some hydrophiine sea snakes. Two character states (17·1 and 26·1) not entirely congruent with the arrangement suggest the relationships of *Laticauda* with particular groups of terrestrial elapines and one hydrophiine (Figs 7b & 7c). Two other character sites (55 and 59) suggest possible relationships between American and Asiatic elapines (Fig. 7d).

It may be concluded that those characters which best survive the Le Quesne test and which indicate the affinities of *Laticauda* with taxa outside the genus are:- 7·1 (marginal lower lip scales), 16·1 (muscular pulmonary air sac), 49 (absence of palatine medial wing). If Le Quesne's procedure is to be viewed as a weighting method (Arnold, 1981) these characters would be given relatively high weight in attempts to reconstruct a phylogeny of laticaudine sea snakes. Out of the various Wagner parsimony runs, run 4 (Fig. 5d) appears to be closest to the topology that would be preferred on the grounds of Le Quesne test results.

Conclusion

Following a study of the morphological evidence using most methods of analysis (some parsimony runs, 'fours', compatibility) it may be concluded that laticaudines and hydrophiines do indeed seem to be comparatively closely related. There is however still a residue of conflicting data which tend to support McDowell's contrasting proposition that *Laticauda* is more closely

Table 12. Le Quesne test: observed/expected failure rates.

Le Quesne's coefficient of character state randomness = Ratio × 100%
Failures: Observed expected ratio

1·1 : 54	57·59	0·94	1·2 : 2	0·67	2·99
2 : 3	31·85	0·09	3 : 29	39·93	0·73
4 : 29	39·93	0·73	5·1 : 4	1·69	2·37
5·2 : 27	10·73	2·52	6·1 : 35	47·33	0·74
6·2 : 43	37·21	1·16	7·1 : 25	52·98	0·47
7·2 : 16	45·82	0·35	8·1 : 31	46·65	0·66
8·2 : 38	47·23	0·8	9 : 29	56·13	0·52
10 : 21	54·09	0·39	11·1 : 49	55·75	0·88
11·2 : 47	50·51	0·93	12·1 : 23	41·86	0·55
12·2 : 52	51·57	1·01	13 : 37	56·32	0·66
14 : 46	54·39	0·85	15 : 30	52·48	0·57
16·1 : 27	56·19	0·48	16·2 : 3	1·06	2·83
17·1 : 13	24·01	0·54	17·2 : 0	–	–
18 : 27	33·7	0·8	19 : 30	55·32	0·54
20 : 36	51·85	0·69	21·1 : 3	30·8	0·1
21·2 : 36	54·49	0·66	23·1 : 33	54·58	0·6
23·2 : 33	28·19	1·17	24 : 37	57·93	0·64
25·1 : 0	–	–	25·2 : 27	51·93	0·52
26·1 : 24	48·64	0·49	26·2 : 31	49·41	0·63
26·3 : 26	41·32	0·63	27 : 0	14·61	0
28·1 : 25	39·24	0·64	28·2 : 22	26·3	0·84
29 : 48	58·97	0·81	30 : 34	50·01	0·68
31 : 24	39·22	0·61	32 : 26	41·8	0·62
33 : 21	40·53	0·52	34 : 3	31·33	0·1
35 : 36	49·32	0·73	36 : 34	59·8	0·57
37 : 34	59·8	0·57	38 : 36	60	0·6
39 : 0	–	–	40 : 3	1·06	2·83
41·1 : 39	47·48	0·82	41·2 : 41	52·03	0·79
42 : 48	39·13	1·23	43 : 40	47·57	0·84
44 : 64	63·28	1·01	45·1 : 27	49·83	0·54
45·2 : 3	1·06	2·83	45·3 : 0	–	–
46·1 : 42	58·72	0·72	46·2 : 56	59·58	0·94
47 : 27	30·62	0·88	48 : 63	66·65	0·95
49 : 29	59·7	0·49	50 : 33	41·39	0·8
51·1 : 4	40·32	0·1	51·2 : 44	61·92	0·71
51·3 : 10	12·09	0·83	52 : 21	26·39	0·8
53 : 37	45·26	0·82	54·1 : 5	11·86	0·42
54·2 : 6	12·36	0·49	55 : 22	49·95	0·44
56 : 48	52·63	0·91	57·1 : 26	41·59	0·63
57·2 : 47	63·58	0·74	57·3 : 21	23·82	0·88
58 : 39	50·5	0·77	59 : 20	49·94	0·4
60 : 56	52·9	1·06	61 : 31	50·62	0·61
62 : 54	64·87	0·83	63 : 57	47·87	1·19
64·1 : 27	24·7	1·09	64·2 : 38	38·82	0·98
65 : 25	60·89	0·41			

Grand total
Failures: Observed expected ratio

1276 1822·01 0·7

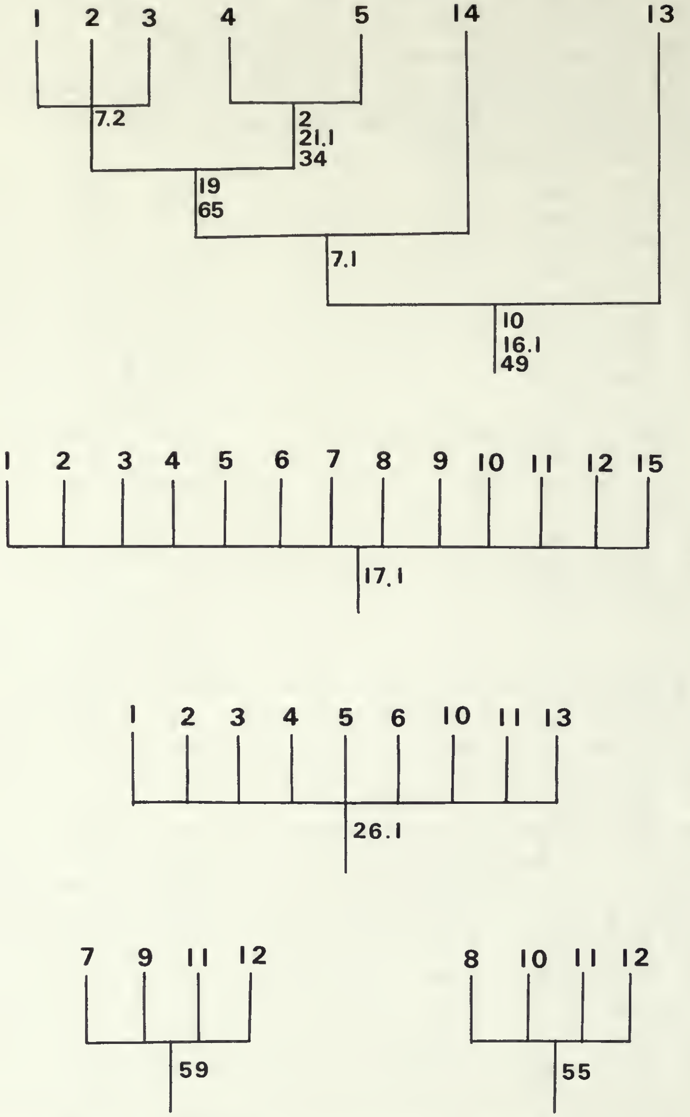

Fig. 7 Le Quesne test cladograms, described by characters having an observed: expected survival ratio <0·5.

related to particular groups of terrestrial elapines than to hydrophiines (a topology suggested both by phenetic analysis and by some parsimony runs).

Evidence from immunology (e.g. Cadle & Gorman, 1981; Mao *et al.*, 1983) and karyology (Mengden pers. comm.) again indicates that the affinities of laticaudines lie with hydrophiines (and Australian terrestrial elapids) although samples tested so far appear not to have included some taxa which McDowell hypothesises to be closely related to *Laticauda* i.e. *Calliophis, Maticora* and *Parapistocalamus.*

The method of sample selection in the present study (Table 4) has led to the terrestrial sample to be rather biased towards Asiatic and American elapids. Given some of the recent evidence provided by biochemical and chromosomal data it would be instructive for future studies further to investigate Australian terrestrial elapids to assess the degree to which the apparent affinity of this group with laticaudines and hydrophiines is corroborated by morphological evidence.

The present assessment of the relationships of laticaudine sea snakes must therefore be that, while the bulk of the evidence examined supports the affinity of laticaudines with hydrophiines, more information is required about the distribution of some characters in order to be able to resolve precisely the relationships of either sea snake group with particular groups within the largely terrestrial Elapinae. The classification recommended by McCarthy (1985) with Elapinae, Laticaudinae and Hydrophiinae treated as equivalent subfamilies of the Elapidae reflects the present lack of clear resolution in the relationships between the three subfamilies, a situation that hopefully will be improved as more morphological, biochemical and karyological information becomes available.

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References

Alvarez del Toro, M. 1982. *Los reptiles de Chiapas* (3rd Edition). Chiapas.

Anderson, J. 1871. On some Indian Reptiles. *Proceedings of the Zoological Society of London.* **1871:** 149–211.

Arnold, E. N. 1981. Estimating phylogenies at low taxonomic levels. *Zeitschrift fur Zoologische Systematik und Evolutionsforschung*. Frankfurt. **19** (1): 1–35.

Boulenger, G. A. 1896. *Catalogue of the snakes in the British Museum (Natural History)* **3.** London.

Cadle, J. E. & Gorman, G. C. 1981. Albumin immunological evidence and the relationships of sea snakes. *Journal of Herpetology* **15** (3): 329–334.

Cogger, H. G. 1975. Sea snakes of Australia and New Guinea. *In* W.A. Dunson, *The Biology of Sea Snakes*: 59–139. Baltimore, London and Tokyo.

Dowling, H. G. & Duellman, W. E. 1978. Systematic Herpetology: A synopsis of families and higher categories. *Publications in Herpetology,* New York. **7.**

Enderman, H. 1970. *A classification of the sea snakes with notes on geographic variation.* Rijksmuseum van Natuurlijke Historie, Leiden (unpublished ms.).

Felsenstein, J. 1981. *Package for inferring phylogenies* (Version 2·0). University of Washington.

—— 1982. Numerical methods for inferring evolutionary trees. *The Quarterly Review of Biology.* **57** (4): 379–404.

Gorman, G. C. 1981. The chromosomes of *Laticauda* and a review of karyotype evolution in the Elapidae. *Journal of Herpetology* **15** (2): 225–233.

Guinea, M. L. 1981. The sea snakes of Fiji. *Proceedings of the Fourth International Coral Reef Symposium*, Manila **2:** 581–585.

——**, Tamiya, N. & Cogger, H. G.** 1983. The neurotoxins of the sea snake *Laticauda schistorhynchus. Biochemical Journal* **213:** 39–41.

Guise, A., Peacock, D. & Gleaves, T. 1982. A method for identification of parallelism in discrete character sets. *Zoological Journal of the Linnean Society* London **74** (3): 293–303.

Kharin, V. E. 1984. Revision of sea snakes of the subfamily Laticaudinae Cope, 1879 Sensu Lato (Serpentes, Hydrophiidae). *In* L.J. Borkin (Ed.) Ecology and Faunistics of Amphibians and Reptiles of the USSR and adjacent countries. *Proceedings of the Zoological Institute, Leningrad.* **124:** 128–139.

Klemmer, K. 1963. Liste der rezenten Giftschlangen. Elapidae, Hydropheidae, Viperidae und Crotalidae. *In* Behringwerk-Mitteilungen, *Die Giftschlangen der Erde*: 255–464. Marburg/Lahn.

Kluge, A. G. 1976. Phylogenetic relationships in the lizard family Pygopodidae: an evaluation of theory, methods and data. *Miscellaneous Publications of the Museum of Zoology, University of Michigan.* **152:** 1–72.

Le Quesne, W. J. 1969. A method of selection of characters in numerical taxonomy. *Systematic Zoology* **18:** 201–205.

—— 1972. Further studies based on the uniquely derived character concept. *Systematic Zoology* **21**: 281–288.

Linnaeus, C. 1758. *Systema Naturae* (10th Edition), **1**. London (Photographic facsimile 1956).

Mao, S.-H. & Chen, B.-Y. 1980. *Sea snakes of Taiwan.* National Science Council, Taipei. Special Publication **4:** xi + 1–62 pp.

——**, Chen, B.-Y., Yin, F.-Y. & Guo, Y.-W.** 1983. Immunotaxonomic relationships of sea snakes to terrestrial elapids. *Comparative Biochemistry and Physiology* **74A** (4): 869–872.

Marx, H. & Rabb, G. B. 1972. Phyletic analysis of fifty characters of advanced snakes. *Fieldiana, Zoology.* Chicago. **63:** viii + 321 pp.

McCarthy, C. J. 1982. *Relationships of the laticaudine sea snakes.* Ph.D. thesis. Council for National Academic Awards (City of London Polytechnic).

—— 1985. Monophyly of elapid snakes (Serpentes: Elapidae). An assessment of the evidence. *Zoological Journal of the Linnean Society,* London. **83:** 79–93.

—— (in preparation). Adaptations of sea snakes that eat fish eggs.

McCoy, M. 1980. *Reptiles of the Solomon Islands.* Wau Ecology Institute Handbook **7:** vi, 1–80 + 20 Pls.

McDowell, S. B. 1967. *Aspidomorphus,* a genus of New Guinea snakes of the family Elapidae, with notes on related genera. *Journal of Zoology,* London. **151:** 497–543.

—— 1969. Notes on the Australian sea snake *Ephalophis greyi* M. Smith (Serpentes: Elapidae, Hydrophiinae) and the origin and classification of sea snakes. *Zoological Journal of the Linnean Society,* London **48:** 333–349.

—— 1972. The genera of sea-snakes of the *Hydrophis* group (Serpentes: Elapidae). *Transactions of the Zoological Society of London* **32:** 189–247.

—— 1974. Additional notes on the rare and primitive sea-snake, *Ephalophis greyi. Journal of Herpetology* **8** (2): 123–128.

Moody, S. M. 1980. *Phylogenetic and historical biogeographical relationships of the genera in the family Agamidae (Reptilia, Lacertilia).* Doctoral Thesis (University of Michigan).

Schlegel, H. 1837. *Essai sur la physionomie des Serpens* (vol. 2). La Haye.

Schneider, J. G. 1799. *Historia Amphibiorum naturalis et literariae* (Fasciculus Primus). Facsimile Edition, Amsterdam.

Slevin, J. R. 1934. The Templeton Crocker Expedition to Western Polynesian and Melanesian Islands, 1933. No. 15. Notes on the Reptiles and Amphibians, with the description of a new species of sea-snake. *Proceedings of the California Academy of Sciences.* Fourth Series. **21** (15): 183–188.

Smith, H. M., Smith, R. B. & Sawin, H. L. 1977. A summary of snake classification. *Journal of Herpetology* **11** (2): 115–121.

Smith, M. A. 1926. *Monograph of the sea-snakes (Hydrophiidae).* London.

—— 1943. *The fauna of British India, Ceylon and Burma including the whole of the Indo-Chinese sub-region.* Reptilia and Amphibia. Vol. 3—Serpentes. London.

Sneath, P. H. A. & Sokal, R. R. 1973. *Numerical Taxonomy.* San Francisco.

Stejneger, L. 1907. Herpetology of Japan and adjacent territory. *Bulletin of the United States National Museum.* Washington D.C. **58:** xvii + 577 pp.

Tamiya, N., Sato, A., Kim, H. S., Teruuchi, T., Takasaki, C., Ishikawa, Y., Guinea, M. L., McCoy, M., Heatwole, H. & Cogger, H. G., 1983. Neurotoxins of sea snake genus *Laticauda. Toxicon* Suppl. **3:** 445–447.

Underwood, G. 1967. *A contribution to the classification of snakes.* British Museum (Natural History) Publication **653.** London.

—— 1982. Parallel evolution in the context of character analysis. *Zoological Journal of the Linnean Society.* London. **74** (3): 245–266.

Villa, J. 1962. *Las serpientes venosas de Nicaragua.* Managua, [only pp. 30–31 seen].

Volsøe, H. 1956. Herpetology of Rennell Island. *Natural History of Rennell Island, British Solomon Islands* **1** (8): 121–134.

—— 1958. Additional specimens of snakes from Rennell Island. *Natural History of Rennell Island, British Solomon Islands* **1** (12): 227–228.

Voris, H. K. 1969. *The evolution of the Hydrophiidae with a critique on methods of approach.* Ph.D. thesis, University of Chicago, [only pp. 368–369 seen].

—— 1977. A phylogeny of the sea snakes (Hydrophiidae). *Fieldiana, Zoology.* Chicago **70** (4): 79–169.

Wolff, T. 1969. The fauna of Rennell and Bellona, Solomon Islands. *Philosophical Transactions of the Royal Society of London. B* **255:** 321–343.

—— 1970. Lake Tegano on Rennell Island, the former lagoon of a raised atoll. *Natural History of Rennell Island, British Solomon Islands.* **6** (61): 7–29.

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British Museum (Natural History)

The Littorinid molluscs of mangrove forests in the Indo-Pacific region

D. G. Reid

Periwinkles (family Littorinidae) are amongst the most intensively studied of marine gastropods, because of their worldwide distribution and abundance in the intertidal environment. This monograph is a comprehensive account of the taxonomy, biology and biogeography of the *'Littorina scabra'* species complex, a hitherto poorly-known group of littorinids ubiquitous in mangrove habitats throughout the Indo-Pacific region. Twenty species are recognized, where most previous authors have distinguished only three. Detailed accounts of the anatomy of each species are given, with particular attention to the reproductive system, by which the species can be reliably distinguished. A key to shells is provided, and 100 figures and plates illustrate the range of shell variation, anatomical characters and geographical distribution of each species.

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In addition to molluscan systematists, this monograph should be of interest to marine biogeographers and ecologists working in the mangrove environment. In recent years much ecological and genetical research has been stimulated by the discovery of sibling species of *Littorina* in Europe. The *Littoraria* species have a similar potential in the Indo-Pacific, where up to ten species may occur sympatrically. Several of the species are polymorphic for shell colour and have already been used as material for the study of mechanisms of natural selection.
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Bernice Brewster

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Introduction

The genus *Hydrocynus* is a member of the Characidae (Order Characiformes) one of the largest families of freshwater fishes found in both Africa and the Neotropics. *Hydrocynus* is, however, endemic to Africa, (see p. 201 for details of distribution). As noted by Weitzman & Fink (1983: 340), the current classification of the characids is problematical. Roberts (1969: 443) divided the African Characidae into the sub-families Hydrocyninae, (to include only *Hydrocynus*) and Alestiinae (to include all remaining African characids). Géry (1977: 18) subsequently erected the family Alestidae to include Roberts's sub-families Hydrocyninae and Alestiinae and restricted the Characidae to include only Neotropical taxa. Géry's (1977) work was not based on a cladistic analysis of the Characidae (*sensu* Greenwood *et al.* 1966) and the characters he used to define the Alestidae appear to be a mixture of plesiomorphies and apomorphies. Vari (1979: 342) included Roberts's Hydrocyninae with the Alestiinae because the latter represented a non-monophyletic assemblage with some of its members being more closely related to *Hydrocynus* than to members of their own sub-family. The current classification of the characids is clearly unsatisfactory but pending further phylogenetic analysis the concept of the Characidae *sensu* Greenwood *et al.* (1966) is followed here.

Species of *Hydrocynus* are pike-like predators, commonly termed 'tigerfishes' for their prominent dentition and dark lateral stripes. The genus was first described by Cuvier (1819) and characterized by him as follows:

> *. . . par des dents peu nombreuses, longues, coniques, très-aiguës tranchantes par les bords, qui se croisent quant la bouche est fermée, et qui ne sont pas recouvertes par les levres. J'en trouve 7 à chaque intermaxillaire, ce qui fait en tout 14 pour la mâchoire supérieure, mais les trois dernières de chaque côté sont beaucoup plus petites que les autres; il n'y en a que 6 de chaque côté à la mâchoire inferieure, et ce sont les deux dernieres qui sont petites. On compte donc 8 grandes dents à chaque machoire. La gueule n'est pas tres fendue, et le maxillaire qui n'a pas de dents se recourbe transversalement sur la commissure. La langue et le palais sont lisses, et les os pharyngiens garnis de dents en velours.*

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With the exception of the teeth overlapping the jaws when the mouth is closed, these characters are applicable to all other members of the Characidae. Valenciennes (1849) added to this list, the presence of an adipose eye-lid, a feature found in other members of the Characidae, such as the African genus *Alestes,* in other characiforms for example the Neotropical families Curimatidae and Hemiodontidae and in unrelated teleosts, notably members of the Clupeidae and Mugilidae.

Boulenger (1907) redefined the genus *Hydrocynus* using the following principal characters: teeth in a single series; a moderately large maxilla which slips beneath the second infraorbital; an elongate body; a large supraorbital bone; a fontanelle present in juveniles, separating the frontals posteriorly and the parietals entirely; a large air-bladder with a posterior chamber about three times the length of the anterior chamber, and a strongly ossified skull. Again, with one exception (see below) these characters are applicable to other members of the Characidae.

Of those characters given by Cuvier (1819) and Boulenger (1907), only two are synapomorphic for species of the genus *Hydrocynus; viz:* moderately large maxilla which slips beneath the second infraorbital; uniserial teeth that overlap the opposing jaw. Roberts (1966, 1967 & 1969) remarked on certain features such as jaw and tooth structure, tooth replacement, posttemporal fossae and presence of an orbitosphenoid tube. On the basis of these characters, Roberts (1966: 215; 1967: 242; 1969: 443) postulated *Hydrocynus* to be related to the African characid genus *Alestes.* However, in the absence of any osteological definition of either *Hydrocynus* or *Alestes,* no evidence could be presented to either corroborate or refute Roberts's hypothesis of relationship between these genera.

There is also confusion concerning the validity of certain currently recognized species of *Hydrocynus.* Boulenger (1909) recognized five species solely on the basis of meristic characters for which there was overlap in the ranges. Boulenger (1901, 1907) commented that two of the recognized species of *Hydrocynus* were so alike that he hesitated to retain them as distinct species. Svensson (1933) also noted the close resemblance between some species; Johnels (1954) also found it very difficult to distinguish the species of *Hydrocynus* and concluded that the taxonomy of the genus was unsatisfactory. Nonetheless, all five species have continued to be recognized despite various authors' misgivings concerning their validity.

The aims of this paper are three-fold. Firstly, to define the genus on osteological characters; secondly to present an hypothesis of relationship to other characiforms by adopting a cladistic approach, and thirdly, to review the taxonomy of the contained species.

Note on the nomenclature

The application of the name *Hydrocynus* to the African tigerfishes has been a subject of controversy. Hasselquist (1757) described a taxon *Salmo dentex* from the Nile, which is now recognized as *Alestes dentex.* Forsskål (1775: 66) identified a Nilotic fish as *Salmo dentex* of Hasselquist. Unfortunately, this specimen is no longer extant (Klausewitz & Nielsen, 1965: 12) but the description and meristic data given by Forsskål are without doubt those of a tigerfish.

Lacepède (1803: 272–273) further confounded the issue as he regarded *S. dentex* of both Hasselquist and Forsskål to be synonyms of *Characinus dentex* (Geoffroy Saint Hilaire in Lacepède 1803). Geoffroy Saint Hilaire (1809) wrote at length of the differences between Hasselquist's *Salmo dentex* and the specimen identified as the same by Forsskål, although he did nothing to resolve the problem. In 1817, Cuvier introduced a new genus, *Hydrocynus* which included in a footnote Forsskål's *Salmo dentex* (*non* Hasselquist). In a later paper, Cuvier (1819: 353–357) gave Forsskål's *Salmo dentex* the name '*Hydrocyon forskahlii*' in an attempt to resolve the confusion that had arisen over the identity of this fish.

Rüppell (1829: 5) subsequently used the binomen *Hydrocyon dentex* for the tigerfish in question. However, Hasselquist's *S. dentex* is not available as the description precedes the starting point of zoological nomenclature (International Code of Zoological Nomenclature 1985: article 3). *Salmo dentex* (as of Forsskål) is not available as a senior synonym for *Hydrocynus forskahlii* under article 49 of the International Code of Zoological Nomenclature.

Materials

The osteology and soft anatomy were studied using ethanol preserved specimens, double stained alcian blue/alizarin red 'S' transparencies (following the procedure detailed by Dingerkus & Uhler, 1977), dry skeleton preparations, and radiographs.

Most of the material used in the preparation of this paper, is held in the British Museum (Natural History) (BMNH) collection, but additional specimens have been examined from the following institutions: Muséum National d'Histoire Naturelle, Paris (MNHN): Musée Royal de l'Afrique Centrale (MRAC); Institut Royal des Sciences Naturelles, Brussels (IRSN); Rijksmuseum van Natuurlijke Historie, Leiden RMNH) and California Academy of Sciences (SU). A detailed list of the material examined is given in the species descriptions, and outgroup material examined is given in Appendix 1.

Note on the measurements

The standard length (SL) is measured from the tip of the snout, including premaxilla, to the region of the caudal peduncle approximating to the posterior margin of the hypural bones. Body depth is measured at the deepest part of the body anterior to the dorsal fin; head length is measured from the tip of the snout, including the premaxilla, to the posterior edge of the operculum; snout length is measured in the horizontal plane from the tip of the snout, including premaxilla, to the anterior margin of the eye. The interorbital width is measured as the greatest width of the frontals between the eyes. The 4th infraorbital is measured at the greatest width from the posterior margin of the eye to the posterior margin of this element. The depth of the premaxilla is measured in the mid-line from its junction with the supraethmoid to the base of the teeth. All measurements are made in millimetres and proportions are expressed as a percentage of the standard length.

The vertebrae are counted as abdominal (including the 4 Weberian elements) and caudal (including the first fused ural and preural centra).

Lateral line scale counts are taken from the first pore-bearing scale posterior to the supracleithrum to the origin of the caudal fin.

Abbreviations used in the figures

AA	anguloarticular
ABH	anterior basihyal
AHY	anterohyal
AO	antorbital
AP	premaxillary ascending process
BB	basibranchial
BO	basioccipital
BSR	branchiostegal rays
C	claustrum
CB	ceratobranchial
CE	centrum
CL	cleithrum
COR	coracoid
CSI	cavum sinus imparis
D	dentary
DHY	dorsohyal
DR	distal radial
DSP	dermosphenotic
ECT	ectopterygoid
END	endopterygoid
EP	epioccipital
EPB	epibranchial
ES	extrascapular
EX	exoccipital
F	frontal
FM	foramen magnum
FR	fin rays
H	hyomandibula
HB	hypobranchial
HP	hypural
HS	hyomandibular spine
HSP	haemal spine
IC	intercalar
ICL	intercalarium
IH	interhyal
IO	infraorbital
IOP	interoperculum
LE	lateral ethmoid
LP	lateral process of centrum 2
M	maxilla
MC	mesocoracoid
MET	metapterygoid

mm1F	maxillary-mandibular ligament facet
MRP	median rostral process
N	nasal
NC	neural complex
NSP	neural spine
OP	operculum
OS	orbitosphenoid
P	palatine
PA	parietal
PB	pharyngobranchial
PBH	posterior basihyal
PC	postcleithrum
PC SB	posterior chamber of the swimbladder
PHY	posterohyal
PLR	pleural rib
PM	premaxilla
POP	preoperculum
PPLR	pleural rib articulating with postero-ventral surface of haemal spine
PRO	prootic
PROX	proximal radial
PS	parasphenoid
PT	pterotic
PTF	posttemporal fossa
PTS	pterosphenoid
PTT	posttemporal
PU	preural centrum
PV	pelvic bone
Q	quadrate
R	radial
RA	retroarticular
S	scaphium
SC	supracleithrum
SCP	scapula
SO	supraoccipital
SOP	suboperculum
SP	sphenotic
SP ST	sphenotic strut
SU	supraethmoid
SUO	supraorbital
SYM	symplectic
TP	toothplate
TR	tripus
V	vomer
VHY	ventrohyal

Osteology of the genus *Hydrocynus*

The description is based on *Hydrocynus forskahlii* Cuvier 1819, type species of the genus. The terminology of Weitzman (1962) is followed, with the following exceptions: vomer for prevomer and intercalar of opisthotic (Roberts, 1969); supraethmoid for ethmoid, and epioccipital for epiotic (Patterson, 1975); anguloarticular for articular, and retroarticular for angular (Nelson, 1973).

Kampf (1961) described the osteology and myology of *H. forskahlii* in a paper concerned with the comparative functional morphology of this species and *Gasterosteus aculeatus, Spinachia spinachia* and *Esox lucius*. I disagree with Kampf's identification and nomenclature of the cranial bones, those labelled prefrontal, prootic, epioccipital, ectethmoid and palatine by Kampf are identified here as supraethmoid, sphenotic, extrascapular, lateral ethmoid, and ectopterygoid respectively. In his figure 27 (p. 424) the bones labelled 'ectopterygoid' and 'endopterygoid' seem to be an endopterygoid that has fractured giving the appearance of two bones. Subsequent figures show this bone to be entire, and labelled as the 'ectopterygoid'.

Neurocranium

In dorsal view the *neurocranium* is tapered, being widest posteriorly.

The *supraethmoid* is a 'T'-shaped bone (Fig. 1A), its stem being slightly shorter than the broad lateral wings forming the cross-bar of the 'T'. The anterior border bears a median rostral process, with a shallow depression in the vertical mid-line. This depression accepts the ascending premaxillary processes while the lateral wings articulate with facets on the premaxillae (see pp. 171–172). The lateral supraethmoid wings are thick, blunt, transverse processes with a ventral curvature. A ligament connects the ventral portion of the lateral supraethmoid wing to the palatine (see p. 175). Each lateral supraethmoid wing rests laterally in the dorsomedial premaxillary facet and contacts the anterior tip of the ascending limb of the maxilla; the whole complex is tightly bound by connective tissue. Ventrally, the supraethmoid and vomer meet at a straight, transverse juncture. The *nasals* are rod-shaped and lie lateral to the supraethmoid.

The *vomer* is a rectangular bone with an elliptical, posteriorly directed process (Fig. 1C). Posterodorsally, the main part of this bone contacts the lateral ethmoid; the dorsal surface of the

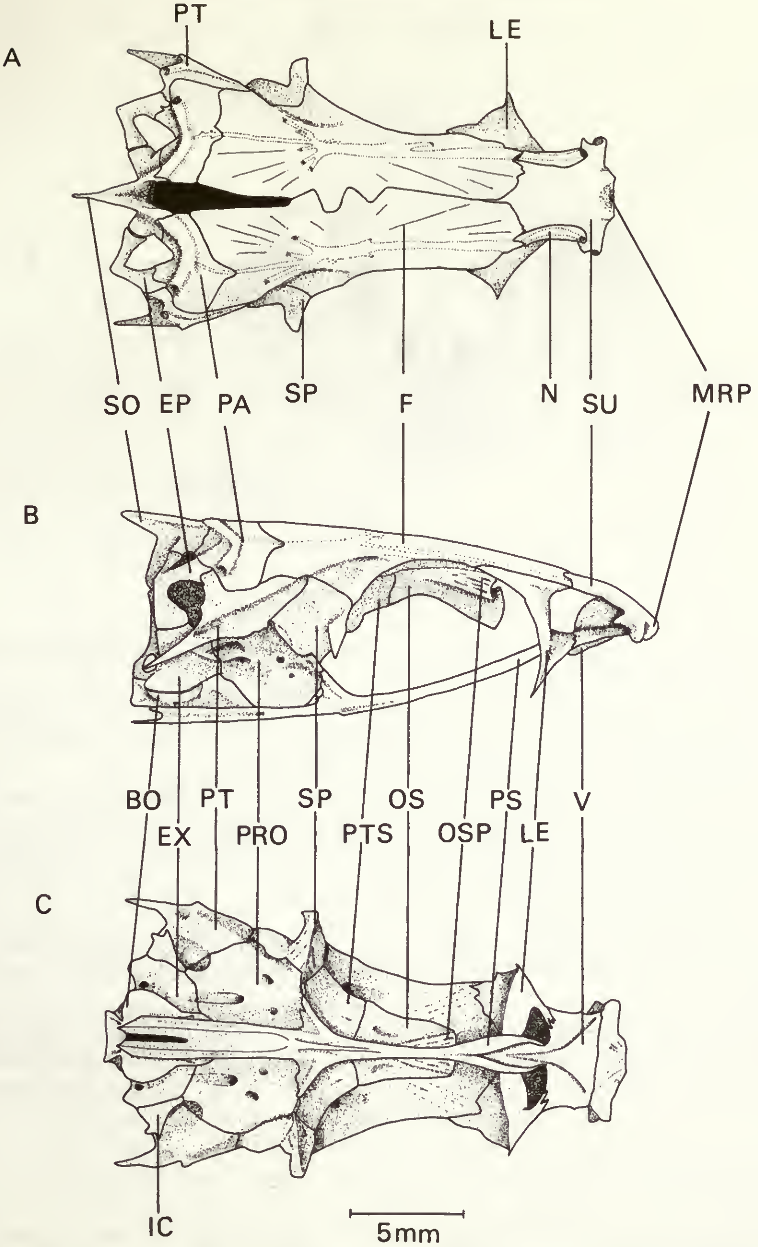


Fig. 1 *Hydrocynus forskahlii* neurocranium: A, dorsal view; B, right side, lateral view; C, ventral view.

posterior process contacts the parasphenoid. Ventrally, the vomer is formed into a 'V' shaped ridge (Fig. 1C), although the development of this ridge appears to be variable.

The *lateral ethmoid* lies beneath the anteroventral portion of the frontal. The paired lateral ethmoid elements contact the supraethmoid cartilage in the mid-line. Each bone has a medially situated foramen for the passage of the olfactory nerve. In some specimens larger than 400 mm SL a tubular ossification extends posteriorly from around the olfactory foramen and contacts the posterior part of the orbitosphenoid process.

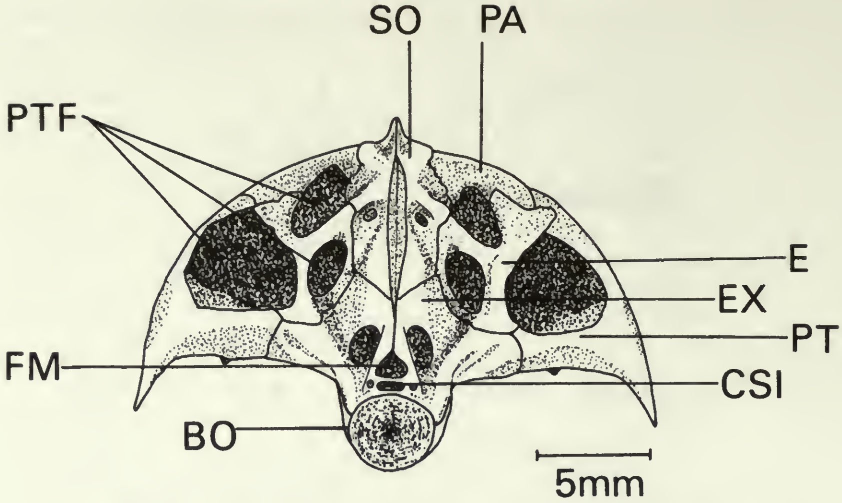


Fig. 2 *Hydrocynus forskahlii* neurocranium, posterior view.

The lateral ethmoid wing projects ventrally from beneath the anterolateral margin of the frontal, forming the anterior wall of the orbit.

The rectangular *frontals* form most of the cranial roof. They are flat dorsally with well-developed striae. The posterolateral part of the frontal contributes extensively to the long dilatator fossa and partially overlaps the fossa's medial border.

In juveniles and specimens up to 300 mm SL, there is usually a medial fontanelle separating the parietals and dividing the posterior margins of the frontals. Posteriorly, the fontanelle is bordered by the supraoccipital. In specimens greater than 300 mm SL, the frontals abut one another posteriorly although the parietals remain separated by a fontanelle which is covered by a thick sheet of connective tissue.

The *parietals* contribute most of the posterior cranial roof and are comma-shaped bones (Fig. 1A). Each parietal contacts the supraoccipital posteromedially the epioccipital posteriorly and the pterotic laterally.

The *supraoccipital* forms the posteromedial part of the cranial roof; it is deeply sulcate and contacts the parietals as described above; its posterolateral borders contact the epioccipitals.

The medial border of each *epioccipital* (Figs 1A & 2) contacts the supraoccipital, while the ventromedial and ventral borders make extensive contacts with the exoccipital. Laterally, the epioccipital makes narrow contact with the pterotic and dorsally it contacts the parietal.

There are three openings into the *posttemporal fossa*, situated dorsally, laterally and medially (Fig. 2). The dorsal opening is bounded by the parietal anteriorly, by the supraoccipital medially, and by the epioccipital laterally; the lateral opening is bounded by the pterotic and epioccipital; the medial opening is contained entirely within the epioccipital.

The *exoccipitals* are irregular in shape (Fig. 2). Each contacts the supraoccipital dorsally and epioccipital dorsolaterally, the pterotic laterally, the basioccipital ventrally and the prootic anteroventrally. Medially, both exoccipitals contact each other dorsal and ventral to the foramen magnum and cavum sinus imparis. The intercalar (see below) lies ventral to the suture between the exoccipital and pterotic. The exoccipital is pierced posterolaterally by the large foramen for the tenth cranial (vagus) nerve. Together, the ventral part of the exoccipital and the dorsal part of the basioccipital form the small, slightly inflated lagenar capsule (Fig. 1B). In specimens up to 120 mm SL the capsule is greatly inflated, a characteristic of all characiforms (see Fink & Fink, 1981: 315). Species of *Hydrocynus*, however, attain a much larger size than most other characiforms, thus the apparently reduced inflation is a negatively allometric phenomenon.

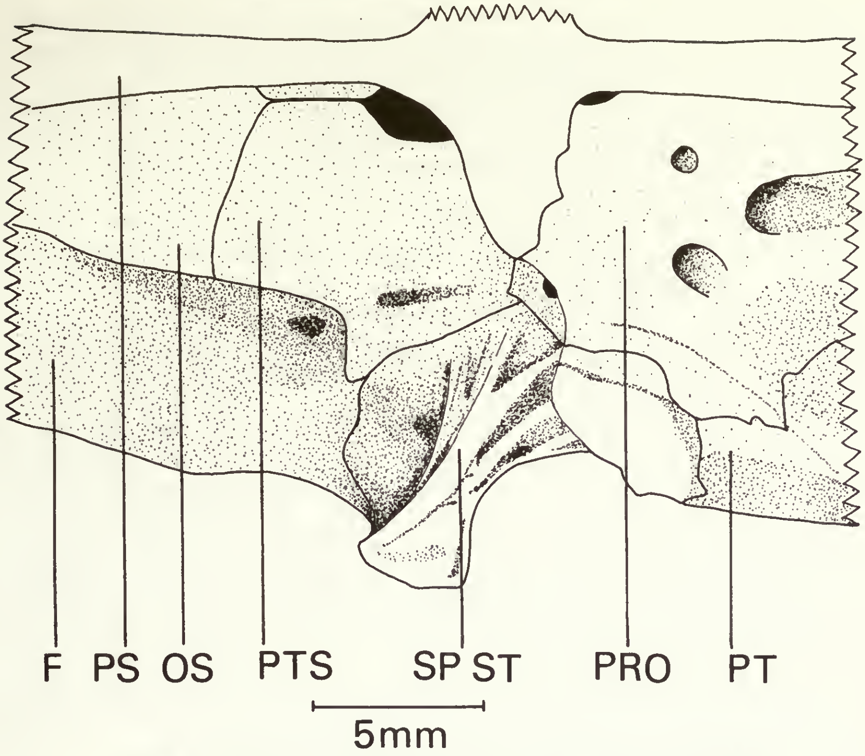


Fig. 3 *Hydrocynus forskahlii* orbito-otic region, ventral view.

The *intercalar* has a flask-shaped outline (Fig. 1C) and lies ventral to the suture between the pterotic and exoccipital, contacting the prootic anteriorly. The intercalar bears a short, thorn-like posterior process which is connected ligamentously to the posttemporal (see p. 179).

The *basioccipital* contributes to the lagenar capsule (see above) and is bordered by the prootics anteriorly; the parasphenoid ventromedially, and the exoccipitals dorsally (Fig. 1B & C). It is divided bilaterally into bony lamellae which contact the parasphenoid ventrally. These lamellae, together with the prootics and posterior part of the parasphenoid form the floor of the large posterior myodome. In specimens up to 600 mm SL the myodome opens ventrally through a deep notch in the posterior section of the parasphenoid (Fig. 1C). This ventral opening closes ontogenetically, in specimens above 600 mm SL, the notched parasphenoid is progressively less evident and in the largest specimens examined is just visible.

Each *pterotic* (Figs 1B & C) forms the posterolateral portion of the cranium and contacts on its side, the parietal and epioccipital posterodorsally, the frontal anterodorsally, the sphenotic anteriorly and the exoccipital, intercalar and prootic ventromedially. The posterolateral surface of the bone contributes to the dilatator fossa, which continues posteriorly as a groove. The pterotic has a long posteroventrally directed spiny process from which originate, anteriorly, the *levator operculi* muscle; ventrally it provides the site of origin for the *protractor pectoralis* muscle, and posterodorsally an insertion for part of the epaxial body musculature.

The ventrolateral surface of the pterotic is deeply idented by the hyomandibular fossa, which articulates with the posterodorsally situated hyomandibular facet.

The *sphenotic* contacts the frontal dorsally, and forms the anterior surface of the long, deep dilator fossa (Fig. 1b). The sphenotic spine forms the posterior margin of the orbit; ventrally it is expanded to form a short thick process (Fig. 1B) from which the *levator arcus palatini* muscle dilator fossa (Fig. 1B). The sphenotic spine forms the posterior margin of the orbit; ventrally it is bone (Fig. 3), the posteromedial edge of which contacts the sphenotic facet. The sphenotic facet articulates with the anterodorsal surface of the hyomandibula.

The *prootics* are large and irregularly shaped, forming most of the cranial floor and wall (Fig. 1C). Anteriorly, each prootic is produced into a ridge which contacts the sphenotic laterally and the ascending process of the parasphenoid medially. The anterior face of the prootic contributes to the posteroventral wall of the orbit, and is pierced by the trigemino-facialis foramen. The anterior faces of the prootics, are connected to one another medially by a sheet of connective tissue that forms the anterior roof to the posterior myodome and separates it from the optic nerve.

The prootic is pierced by a number of foramina, of which, the circular jugular foramen continues posteriorly as the jugular groove across the posterior surface of the prootic and anterior margin of the exoccipital (Fig. 1C).

The subtemporal fossa is a shallow depression extending from the posterior part of the prootic to the suture between the prootic, exoccipital, intercalar and pterotic bones, the deepest part of the fossa lying at the point of this suture. The *adductor hyomandibulae* and *adductor operculi* muscles originate from the subtemporal fossa.

The *pterosphenoid* bones are roughly hexagonal in shape, contact each other anteromedially and form part of the posterior wall of the orbit. Posteromedially, each pterosphenoid is separated from its partner by the foramen for the optic nerve, which is floored ventrally by the horizontal sheet of connective tissue that extends between the prootics (see above).

The *orbitosphenoid* is a rectangular bone which contacts the pterosphenoid posteriorly and frontal dorsally; a tubular process (Fig. 1B & C), encloses the olfactory bulb and posterior end of the olfactory nerve. In some large specimens (400 mm SL or more), the orbitosphenoid process is sutured to a similar tubular process that extends from the lateral ethmoid posteriorly (see p. 167). The olfactory nerve is thus entirely enclosed.

The *parasphenoid* is a stout, elongate bone that contacts the vomer anteroventrally, and the prootic and basioccipital posterolaterally (Fig. 1C). The ascending processes of the parasphenoid are convex where they meet the prootic.

Jaws

In lateral view, the *lower jaw* is elongate, roughly triangular and deepest posteriorly, where the dorsal surface is rather convex (Fig. 4). The *dentary* tapers anteriorly and is joined to its partner by an interlocking symphysial hinge (described by Eastman, 1917). The medial wall of the dentary contains a roofed over replacement tooth trench, that is pierced by large foramina

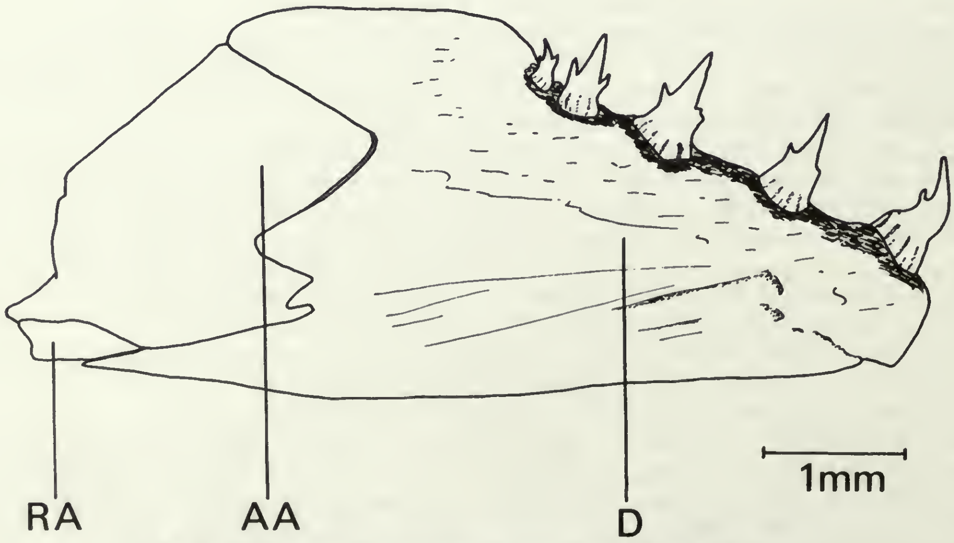


Fig. 4 *Hydrocynus forskahlii* lower jaw, right side, lateral view.

immediately above each replacement tooth (see Roberts, 1967: 233). The trench is referred to herein as 'replacement cavities' in preference to 'trench' because the individual replacement teeth are compartmentalized as opposed to being compressed together in an open trench, as in other African characids. There are five tooth replacement cavities, the anterior four each containing a single large tooth, whereas the fifth may contain one or two small, usually tricuspid teeth. The replacement teeth are directed posterodorsally with their tips just protruding above the rim of the replacement cavity. The functional teeth are widely and evenly spaced along the dorsal border of the dentary.

Posteriorly, the dentary is sutured to the *anguloarticular*, the latter having a diarthritic joint with the quadrate. Meckel's cartilage lies between a small posterior process on the anguloarticular and an anterior dentary process. The small triangular coronomeckelian bone lies dorsal to Meckel's cartilage on the anteromedial surface of the anguloarticular. The posteroventral edge of the anguloarticular is grooved to accommodate the small, wedge-shaped *retroarticular*.

The posterolateral surfaces of the dentary and anguloarticular are broadly recessed to accommodate the maxilla.

The *premaxillae* are elongate bones, each bearing 6 or 7 functional teeth, and are united anteromedially by a symphysial hinge. Unlike the halves of the lower jaw, the premaxillae do not interlock but have a syndesmotic connection. As in the dentary, the tooth replacement trench is roofed over and partitioned into usually five replacement cavities. The posterior cavity may contain two or more small, tricuspid replacement teeth; the other four cavities each contain a single large conical tooth. The replacement teeth are orientated posterodorsally within the cavities, with their tips just projecting beyond the rim. The functional teeth are widely and evenly spaced along the ventral border of the premaxilla.

The ascending process of the premaxilla is a short, square blade with a small dorsal notch (Fig. 5). Posteromedial to the ascending process there is an articular fossa, which articulates with the lateral border of the supraethmoid process. A second, dorsomedially situated facet accommodates the lateral supraethmoid wing. This coupling of the supraethmoid and premaxillae forms a condylar joint permitting a limited dorsoventral rotation of the upper jaw.

Distally, the premaxilla is very deep and its dorsomedial surface is grooved to accommodate the ascending limb of the maxilla. Posteroventrally, the premaxilla and maxilla are ankylosed, although they can be separated in specimens up to 100 mm SL.

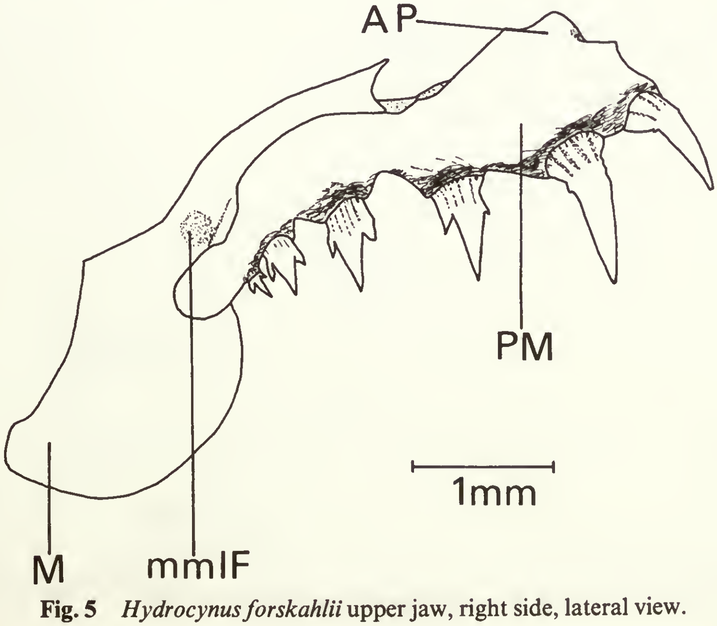


Fig. 5 *Hydrocynus forskahlii* upper jaw, right side, lateral view.

The *maxilla* is an edentulous, lamellar bone with an anteriorly curved, ascending process that rests on the premaxilla (see above; Fig. 5). The anterolateral face of the maxilla bears a small depression to which the maxillary-mandibular ligament is attached. Dorsomedially, the posterior margin of the maxilla has a small cup-shaped protuberance onto which insert some dorsomedial fibres of the *adductor mandibularis* muscle.

Teeth

The smallest alizarin/alcian blue stained specimens examined (16 mm, 22 mm, 23 mm and 25 mm SL (BMNH 1981.2.17: 2600–2609)) display a transition from a conical to tricuspid dentition. The 16 mm SL specimen is heterodont, with 14 upper and 8 lower jaw teeth, of which 2 on either side of the upper jaw and a single tooth on the lower jaw are tricuspid. The remaining teeth are all conical in the upper jaw and right dentary (Fig. 6), but are bicuspid in the left dentary. The conical juvenile teeth are simple, uniseriate, translucent and, in the upper jaw they contact one another, thus closely resembling the conical dentition of the dwarf characid, *Lepidarchus adonis*.

This 16 mm specimen has 8 upper and 6 lower tricuspid replacement teeth, which lie medial to the functional dentition. Each tricuspid replacement tooth can be separated into three conical elements, thus suggesting that such teeth are formed by the fusion of 'juvenile' conical elements (see also p. 187).

The 22 mm SL specimen retains a conical tooth on each side of the upper jaw, which closely contacts the anterior second tricuspid tooth; all other functional and replacement teeth are tricuspid. Diastemata separate the functional teeth.

The 23 and 25 mm SL specimens have a functional and replacement dentition of 12 upper and 8 lower tricuspid teeth. A specimen of 40 mm SL has conical teeth anteriorly in both jaws but

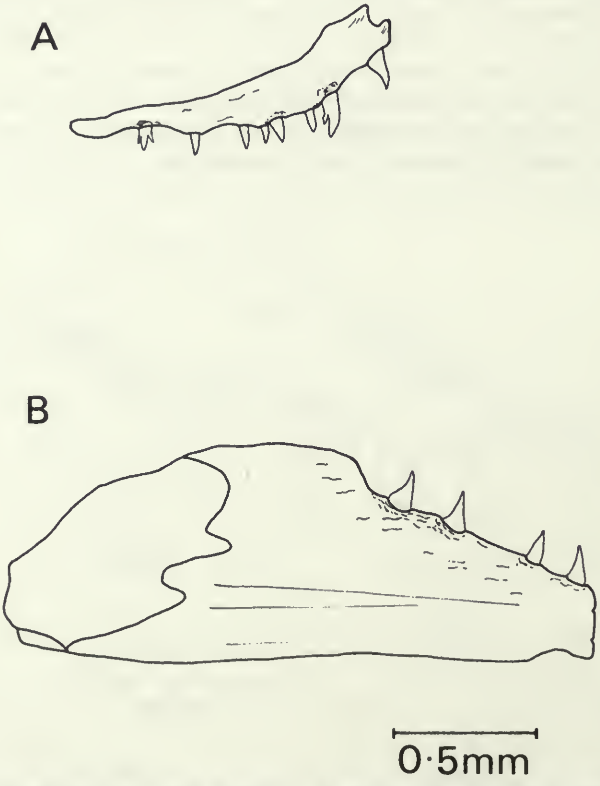


Fig. 6 *Hydrocynus forskahlii* 16 mm SL specimen: A, premaxilla, right side, lateral view; B, lower jaw, right side, lateral view.

each tooth has lateral cusps in the form of very small, nipple-like protuberances. The posterior teeth of this specimen are all tricuspid with well-developed lateral cusps.

In specimens larger than 50 mm SL the lateral cusps on the anterior teeth are difficult to detect but the teeth at the posterior margin of each jaw are always tricuspid (see also p. 187).

The attachment of the teeth to the jaw is type 1 (*sensu* Fink, 1981), that is they are completely ankylosed to the bone.

Circumorbital series

The *antorbital* is a small ovate bone tightly bound by connective tissue to the anteroventral margin of the supraorbital and the posterodorsal margin of the first infraorbital.

The *first infraorbital*, or lachrymal, is a triangular bone that lies lateral to the posterior third of the premaxilla. Dorsally it contacts the antorbital (see above), and ventrally the second infraorbital. The laterosensory canal runs through the orbital margin of the circumorbitals.

The *second infraorbital* is very large and covers the posteroventral surface of the upper and posterodorsal surface of the lower jaws, and lying lateral to the posterior surface of the maxilla (Fig. 7). Ventromedially, the second infraorbital is secured to the posterior margin of the anguloarticular by a sheet of connective tissue which also covers the maxillary-mandibular ligament. Posteriorly, the second infraorbital contacts the third infraorbital.

The *third infraorbital* is extensive, covering most of the cheek musculature. The *fourth* and *fifth infraorbitals* are also large but, unlike the others, are rectangular. The fifth infraorbital contacts the sphenotic spine anteromedially.

The *dermosphenotic* (sixth infraorbital) is ovoid, posterodorsally curved, and contacts the frontal dorsally, where that bone is indented by the dilatator fossa. The dermosphenotic covers the posterior part of the *dilatator operculi* muscle. The laterosensory canal bifurcates in the dermosphenotic; the anterior branch is continuous with the supraorbital canal, the posterior branch contacts the parietal canal and the ventral branch communicates with the canal of the 5th infraorbital.

The *supraorbital* is an elongate bone that lies anterior to the dermosphenotic. It has extensive contact with the lateral margin of the frontal and contacts the antorbital anteriorly (see above).

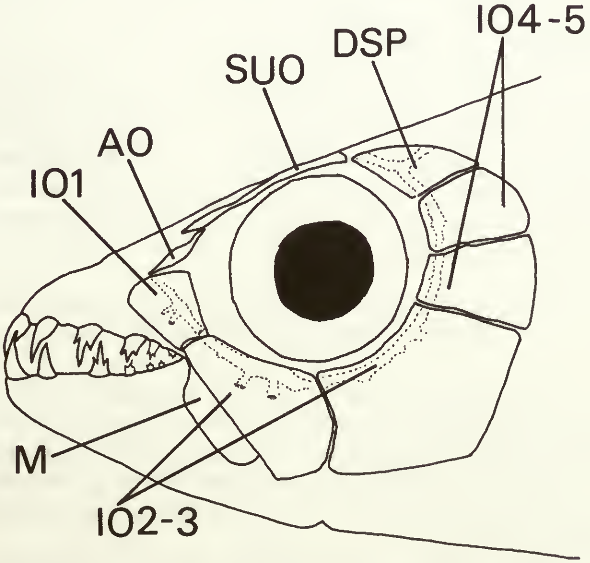


Fig. 7 *Hydrocynus forskahlii* circumorbital series, left side.

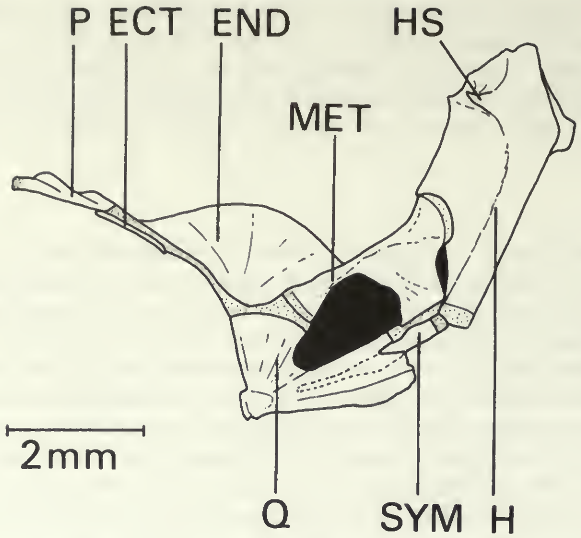


Fig. 8 *Hydrocynus forskahlii* hyopalatine arch, left side, lateral view. Stippling represents cartilage.

Hyopalatine arch

The *hyomandibula* is roughly rectangular in outline, with a strong posterodorsally inclined shaft (Fig. 8). It has a long dorsal condylar articulation with the cranium, and posteriorly, a condylar articulation with the operculum. There are two points of contact between the hyomandibula and metapterygoid (Fig. 8). The anterior edge contacts the short posterior arm of the metapterygoid, and the anteroventral surface of the shaft contacts the posteroventral angle of the metapterygoid. An elongate and narrow, near crescentic foramen separates the hyomandibula and metapterygoid between these points of contact (Fig. 8). The posterodorsal edge of the hyomandibular shaft is deeply grooved to accommodate the anterodorsal edge of the ascending arm of the preoperculum. Ventrally, the hyomandibular shaft lies medial to the preoperculum.

There is a distinct anterolaterally directed dorsolateral spine on the hyomandibula (Fig. 8), which separates the *dilatator operculi* and *levator arcus palatini* muscles.

The *metaptergoid* is axe-shaped in outline (Fig. 8), with a short, rounded posterior arm, a broad ventral arm and a long, anteriorly expanded anterior arm; it contacts the hyomandibula in two places (see above). Its ventral edge is capped with cartilage and contacts the margin of the symplectic and the cartilaginous interface between the latter and the hyomandibula (Fig. 8). A strip of cartilage connects the posterodorsal margin of the quadrate to the cartilage of the ventral arm. The anterior arm lies lateral to the posterior surface of the endopterygoid (Fig. 8), and anteriorly contacts the posterodorsal edge of the vertical limb of the quadrate at a cartilage interface.

The *symplectic* (Fig. 8) is an elongate, tapered bone that lies in a groove on the medial surface of the horizontal limb of the quadrate. Posteriorly, it contacts both the hyomandibula and metapterygoid (see above).

The *quadrate* is an 'L'-shaped element (Fig. 8). The horizontal limb lies lateral to the anterodorsal surface of the preopercular horizontal arm. Posteromedially, there is a deep groove in the quadrate which accommodates the symplectic (see above). The ventrolateral surface of the horizontal limb of the quadrate is formed into a prominent ridge which, anteriorly, forms the lateral facet of the stout articulatory condyle. A strip of cartilage connects the anterodorsal edge of the quadrate to the palatine (Fig. 8).

The *metapterygoid-quadrate fenestra* is ovate and bordered by the metapterygoid and quadrate. The fenestra is filled by a sheet of connective tissue.

The *endopterygoid* is a fan-shaped bone. Its borders lie medial to the metapterygoid, quadrate and to the cartilaginous strip connecting the quadrate and palatine (Fig. 8). A sheet of connective tissue joins the dorsal edge of the endopterygoid to the ventral border of the parasphenoid.

The *ectopterygoid* is a small, edentulous and thin disc, which lies on the anteroventral margin of the palatoquadrate arch (Fig. 8). Anteriorly, it contacts, and is ligamentously joined to, the posteroventral edge of the palatine. The ectopterygoid and palatine are tightly bound by connective tissue.

The *palatine* is an approximately rectangular block of bone, its cartilaginous head articulating with the lateral facet on the lateral wing of the supraethmoid (see p. 166). The palatine head is also ligamentously secured to the supraethmoid and to the ventral surface of the vomer.

Opercular series

The *operculum* is roughly triangular, with an anteromedially situated condyle for articulation with the hyomandibula. Its ventral surface lies lateral to the suboperculum, whereas the anterior margin lies medial to the vertical limb of the preoperculum. Anteroventrally, the operculum contacts and is slightly overlapped by the interoperculum.

The *preoperculum* is crescentic, with a well-developed lateral sensory canal in both the vertical and horizontal arms (Fig. 9). The anterodorsal surface of the horizontal arm lies medial to the quadrate. A short ligament connects the anteroventral tip of the horizontal arm to the retroarticular. Ventrally, the horizontal preopercular arm lies lateral to the interoperculum.

The vertical arm of the preoperculum lies lateral to the hyomandibular shaft anteriorly, and to the operculum posteriorly.

The *interoperculum* is a long, anteriorly tapered bone (Fig. 9). The dorsal margin has two slight protuberances which contact the preoperculum posteriorly and the ventral surface of the quadrate anteriorly. Posteriorly the interoperculum lies lateral to the anterior edge of the suboperculum. Medially, the interoperculum is held in place by a connective tissue sheet which surrounds the opercular series.

The *suboperculum* is a long posteriorly tapered bone, with a small anterodorsal process (Fig. 9). The posterior and ventral edges of the subopreculum are poorly ossified.

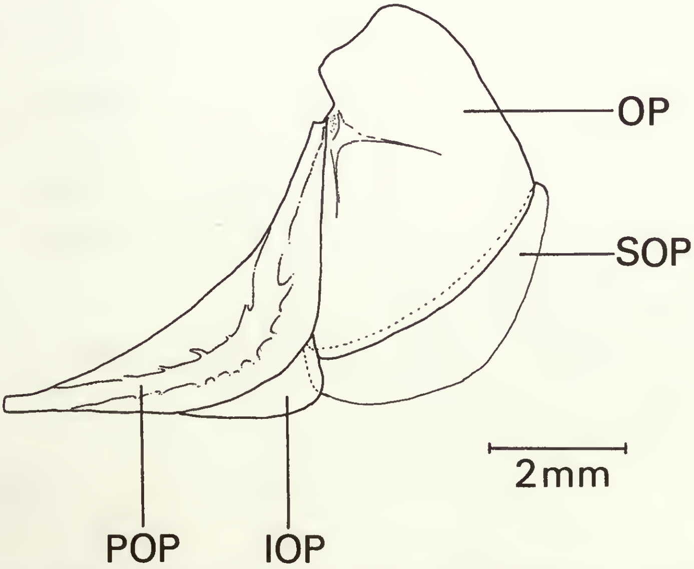
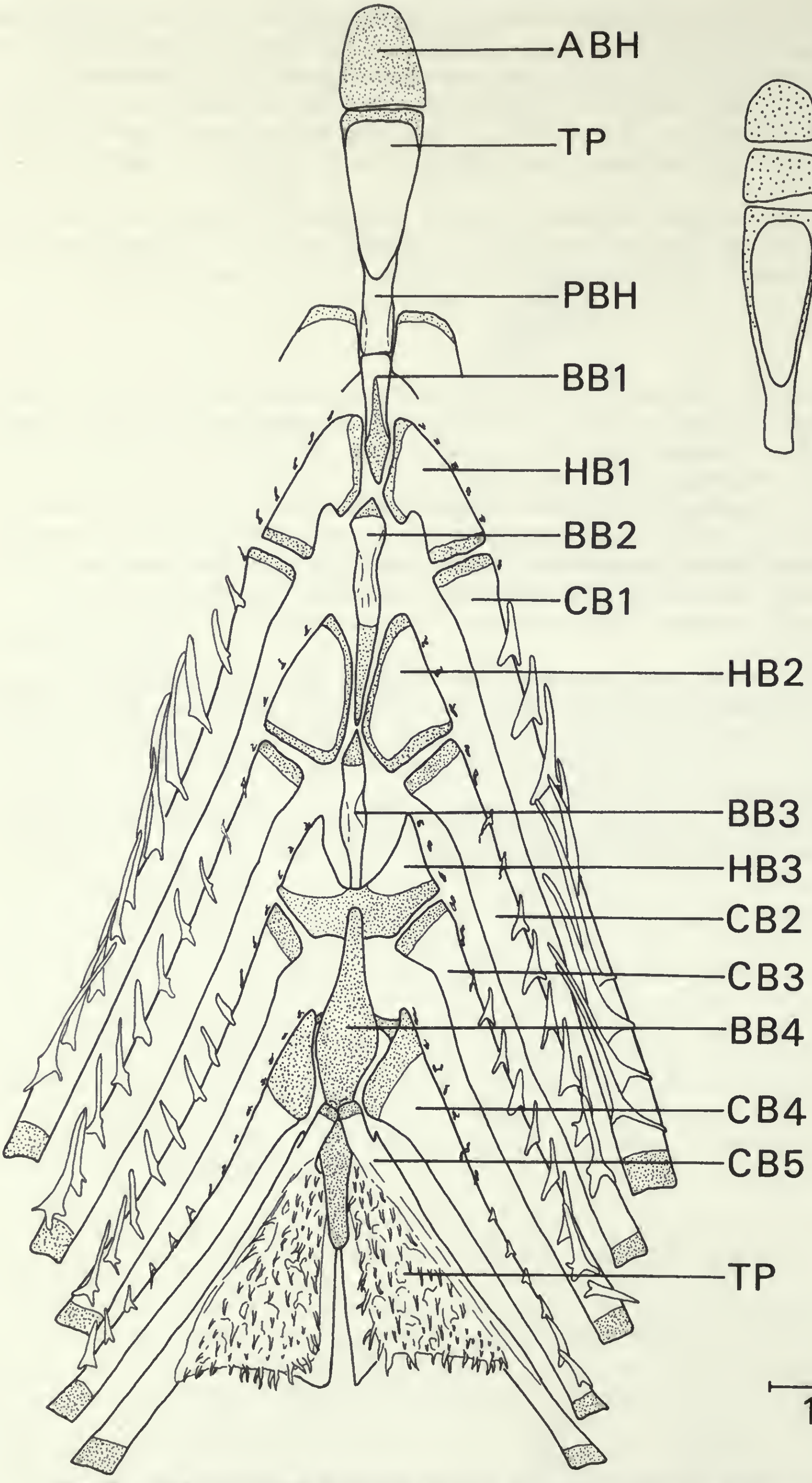


Fig. 9 *Hydrocynus forskahlii* opercular series, left side, lateral view.


ABH
TP
PBH
BB1
HB1
BB2
CB1
HB2
BB3
HB3
CB2
CB3
BB4
CB4
CB5
TP
1mm

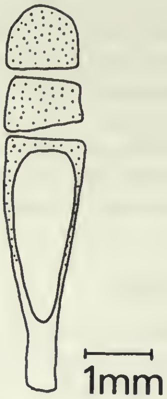


Fig. 10 *Hydrocynus forskahlii* lower gill arch, dorsal view. Stippling represents cartilage.
Fig. 11 Upper right: *Hydrocynus goliath* fragmented basihyal, dorsal view.

Hyoid and branchial arches

The *basihyal* is fragmented; anteriorly a dome-shaped cartilage bloc articulates with the larger, partially ossified posterior section of this element (Fig. 10). In some specimens larger than 100 mm SL the anterior basihyal element is represented by two cartilage blocs; the anterior one is dome-shaped and articulates with a second and square cartilage bloc which, in turn, articulates with the larger posterior section (Fig. 11). The posterior element is connected to the anterior cartilage bloc(s) by dense connective tissue. A ligament connects the dorsolateral surface of the ventrohyal to the connective tissue of the posterior basihyal element and anterior cartilaginous element or elements.

The posterior section of the basihyal is spatulate, ossified posteriorly but cartilaginous anteriorly (Fig. 10); its anterodorsal surface lies below a large elongate, ovoid edentulous toothplate (Fig. 10). Posteriorly, this section of the basihyal articulates laterally with both the first basibranchial and with each dorsohyal.

The *dorsohyal* (Fig. 12) is an axe-shaped bone, which articulates anteromedially with the posterior basihyal element, just anterior to the articulation between the latter and the first basibranchial. The dorsohyal is surrounded by connective tissue which also connects this element to the posterior, ossified section of the basihyal. Posteriorly, the dorsohyal contacts the anterohyal at a cartilage interface. The dorsohyal contacts the ventrohyal anteroventrally.

The *ventrohyal* (Fig. 12) is rectangular, with a prominent anteroventral process. The anterior surface of the process is connected by a short, strong ligament to an anterolateral facet on the urohyal. The ventrohyal contacts both the dorsohyal anterodorsally and the anterohyal posteriorly at a cartilage interface.

The *anterohyal* (Fig. 12) is waisted in lateral view, with a finger-like process anterodorsally that lies between the dorso- and ventrohyals. A blood vessel enters the anterohyal posteriorly, passes through a dorsolateral canal and emerges anteriorly at the ventromedial surface of the finger-like process.

The *posterohyal* is quadrilateral; its ventral surface capped with cartilage which is continuous anteriorly with the cartilage interface between the postero- and anterohyals. The blood vessel associated with the anterohyal (see above) passes medial to the posterodorsal surface of the posterohyal, enters the large foramen which pierces the posterohyal dorsally, to run across the lateral surface of this bone and the cartilage interface before entering the anterohyal canal.

The *interhyal* is a short, rod of bone with a lateral cartilaginous cap, it articulates with the medial face of the posterohyal and is connected *via* a short ligament to the cartilage interface of the hyomandibula, symplectic and metapterygoid laterally.

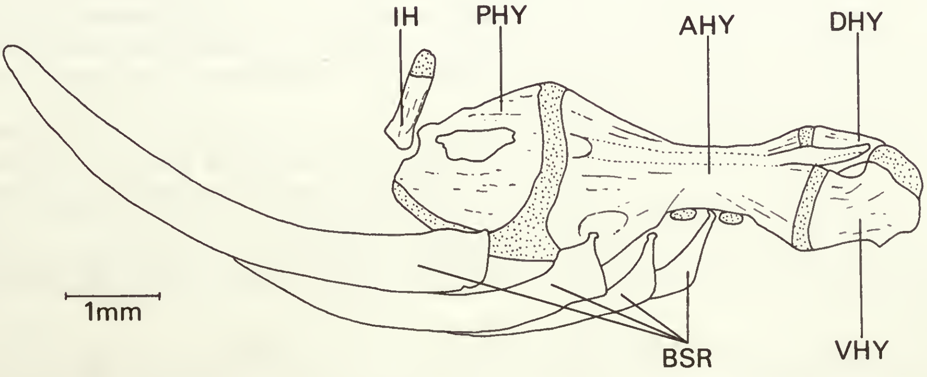


Fig. 12 *Hydrocynus forskahlii* hyoid arch right side; lateral view; basihyal not included.

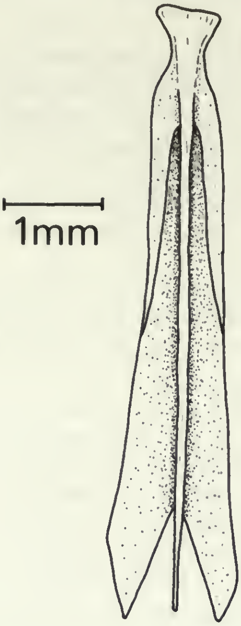


Fig. 13 *Hydrocynus forskahlii* urohyal, dorsal view.

The *urohyal* is elongate, club-shaped and is trifurcate posteriorly (Fig. 13). Its anterior surface is formed into two facets which are ligamentously connected to the anteroventral processes of the ventrohyals (see above, p. 177).

The *first branchiostegal ray* articulates with the ventral surface of the anterohyal cartilage blocs which contact that element.

The *second branchiostegal ray* articulates with the posteroventral surface of the anterohyal.

The *third branchiostegal ray* articulates in a lateral fossa on the posterolateral surface of the anterohyal.

The *fourth branchiostegal ray* articulates with the anteroventral surface of the posterohyal.

Basibranchial 1 (Fig. 10) is peg-shaped, articulating with the basihyal anteriorly; with each first hypobranchial laterally; there is no apparent contact between the first and second basibranchials. Posteriorly, the bone has an arrow-shaped cartilage cap.

Basibranchial 2 is elongate with a triangular cartilaginous cap anteriorly and a rod of cartilage posteriorly, with whose posterolateral surfaces the second pair of hypobranchials articulate. Posteriorly, basibranchial 2 contacts the triangular cartilage cap of *basibranchial 3*. The latter bone is also elongate, with a posterior rod of cartilage ventral to the third hypobranchial cartilage bloc (see below). The anterior cartilage cap of basibranchial 3 articulates with the posteromedial surfaces of the second hypobranchial (Fig. 10).

Basibranchial 4 (Fig. 10) is elongate and cartilaginous. Anteriorly, it lies dorsal to the cartilage bloc of the 3rd hypobranchial (see below). Laterally, basibranchial 4 articulates with ceratobranchial 4; the latter also has a thumb-like process that contacts basibranchial 4 ventrally. Posteriorly, the 4th basibranchial is produced into a rod-shaped process which has a pair of dorsal fossae in which the paired 5th ceratobranchials articulate. The posterior process of this basibranchial lies in the mid-line between the tooth plates fused to the paired 5th ceratobranchials (Fig. 10).

Hypobranchial 1 is roughly hook shaped, and *2* is a triangular element.

The ossified elements of *hypobranchial 3* are roughly triangular in outline and joined posteriorly by a large 'W'-shaped cartilage bloc, which is sandwiched between the posterior cartilage elements of basibranchial 3 ventrally and the anterior part of basibranchial 4 dorsally (Fig. 10).

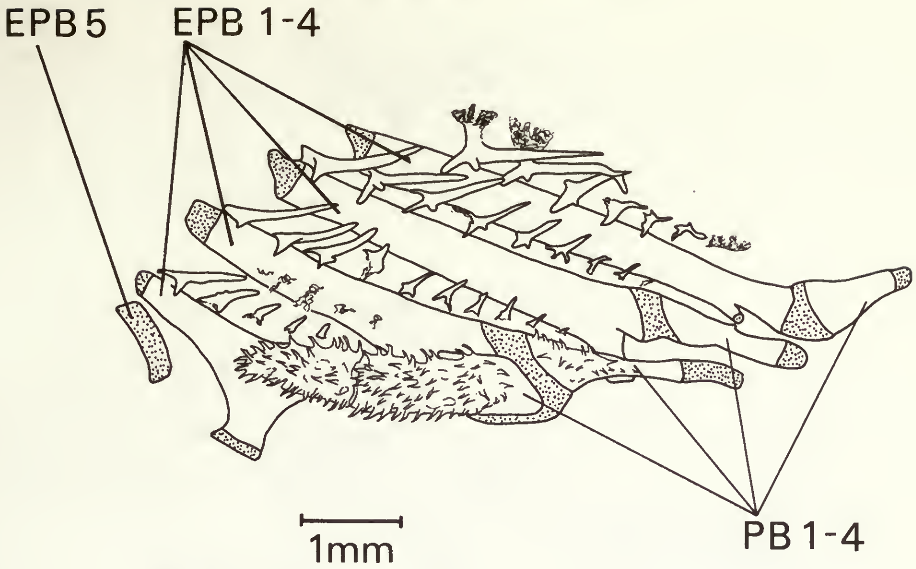


Fig. 14 *Hydrocynus forskahlii* upper gill arch, ventral view.

Ceratobranchials 1–5 are all similar, rod-shaped elements. Ceratobranchials 1–3 articulate anteriorly with their respective hypobranchials, but ceratobranchials 4 and 5 both articulate with basibranchial 4. Anteriorly, ceratobranchial 4 has a large cartilage cap, with an anteroventrally directed thumb-like process that contacts the ventral surface of basibranchial 4 (see above, p. 178).

Epibranchials 1–3 are rod-shaped (Fig. 14). The first has a short uncinate process which articulates with a ventral process on pharyngobranchial 2. Epibranchial 2 has a short anteroventral uncinate process that articulates with a ventral process on pharyngobranchial 3. Epibranchial 3 articulates with the posterior edge of pharyngobranchial 2, the anterior edge of pharyngobranchial 3 and through an uncinate process with the ventral surface of the cranium.

Epibranchial 4 is a triangular-shaped bone, and *epibranchial 5* (Fig. 14), is a short, cartilaginous rod.

Pharyngobranchial 1 is cone-shaped; it contacts the ascending arm of the parasphenoid dorsally and epibranchial 1 posteriorly.

Pharyngobranchial 2 is a rod-like bone with a small oval plate bearing a few small conical teeth fused to its surface ventrally.

Pharyngobranchial 3 is triangular; fused onto its ventral surface there is a triangular toothplate bearing small conical teeth.

Pharyngobranchial 4 is rectangular, with two large tooth plates bearing small conical teeth fused to the ventral surface.

Pectoral girdle

The *extrascapula* (Fig. 15) is an ovate bone that contacts both the parietal and pterotic. Posteriorly, it overlaps the posttemporal laterally. The sensory canal is bifurcate.

The *posttemporal* (Fig. 15) is triangular; dorsally, its apex lies posterior to the parietal. Medially, there is a short and thick process which is connected ligamentously to the intercalar (see p. 169).

The *supracleithrum* is an elongate bone with short and broad dorsal process which lies across the posteromedial surface of the posttemporal (Fig. 15). Ventromedially, and immediately posterior to the apex of the ascending limb of the cleithrum, the supracleithrum is connected to the basioccipital by Baudelot's ligament.

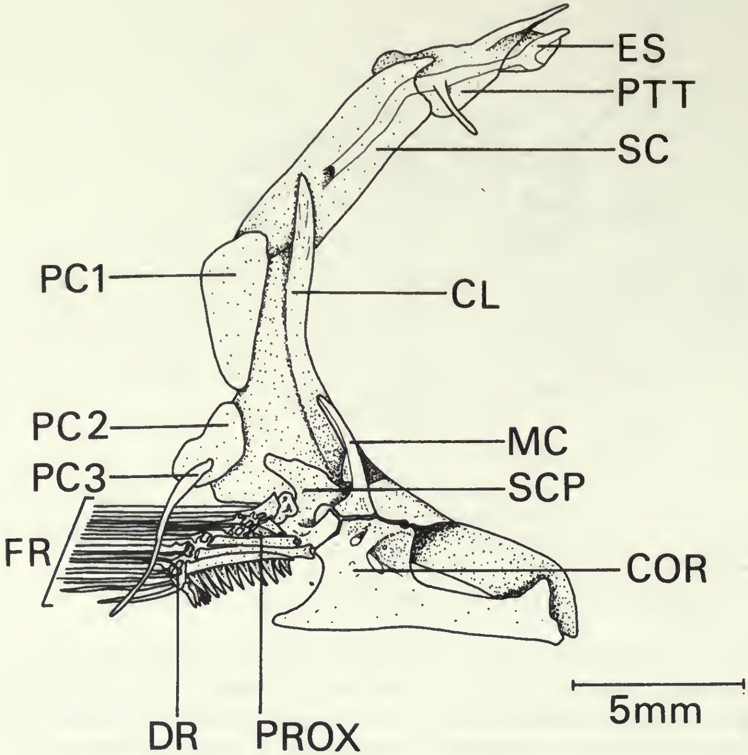


Fig. 15 *Hydrocynus forskahlii* left pectoral girdle, medial view.

The *cleithrum* (Fig. 15) is an 'L'-shaped element. The ascending limb contacts the medial surface of the supracleithrum dorsally and the anterolateral surfaces of postcleithra 1 and 2 posteriorly (see below).

The horizontal limb has a posteromedial shelf-like process with synchondritic connection to the scapula. The posteromedial edge of this shelf-like process has a hook-shaped extension which interlocks with the anterodorsal edge of the dorsal coracoid process (Fig. 15). Anteromedially, the horizontal limb of the cleithrum contacts the apices of the coracoid and the opposing cleithrum.

Postcleithrum 1 is ovate, *postcleithrum 2* is a small palette-shaped element the greater part of which lies medial to the posteroventral surface of the cleithrum, *postcleithrum 3* is a long, rod-shaped bone that contacts the medial surface of postcleithrum 2.

The *scapula* (Fig. 15) has an irregular, near anvil-shaped outline and surrounds a large scapular foramen, the anterior border of which is very narrow. A short, dorsally directed scapular process contacts the mesocoracoid. Posterodorsally, two of the proximal pectoral fin radials articulate directly with the scapula.

The *mesocoracoid* (Fig. 15) is triangular with a long, dorsal process, the ventral part of which spans the scapular foramen.

The *coracoid* is shaped like a jack plane (Fig. 15). Posterodorsally it contacts the mesocoracoid and scapula, and a thick band of connective tissue joins it to the 3rd and 4th proximal radials.

There are four *proximal radials*. The first articulates posteriorly with the first three distal radials, whereas, the others each articulate posteriorly with a single distal radial. The 1st and 2nd proximal radial contact each other laterally and articulate anteriorly with the scapula. The 3rd and 4th proximal radial are tightly bound by connective tissue to the coracoid (see above).

There are six hour-glass shaped *distal radials*. The 3rd bifurcates posteriorly, and the 6th is cartilaginous.

Pelvic girdle

The *pelvic bone* (Fig. 16) is a large triangular element with a short, posteriorly directed, ischiac process. Medially, the two pelvic bones are connected by a short, broad ligament. Posteriorly, the radial elements of the fin articulate with the pelvic bone although the first ray articulates directly with the pelvic bone.

There are three radial elements. The first two are anvil-shaped, the third comma-shaped, with a short, thumb-like process medial to the fin rays.

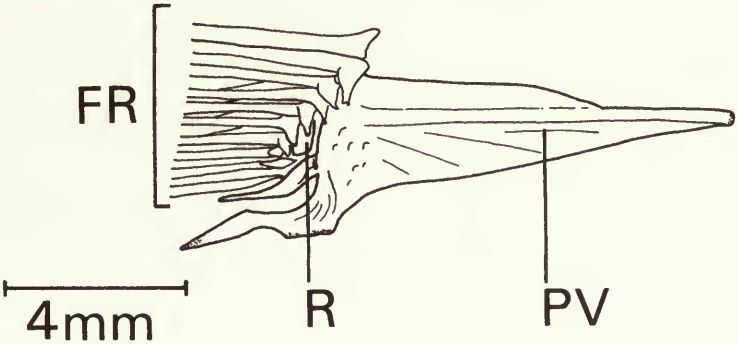


Fig. 16 *Hydrocynus forskahlii* left pelvic girdle, dorsal view.

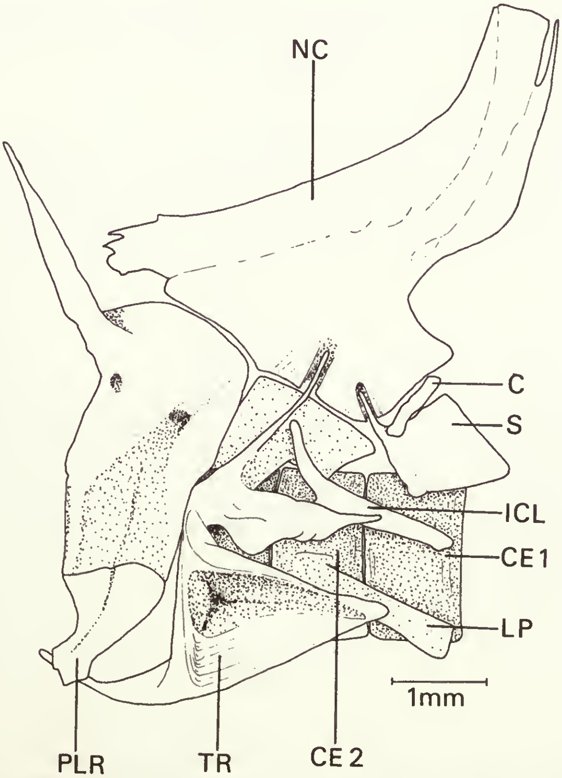


Fig. 17 *Hydrocynus forskahlii* Weberian apparatus, right side, lateral view.

Vertebrae

There are 28–32 abdominal vertebrae, most of which support pleural ribs. The first four contribute to the Weberian apparatus and support the Weberian ossicles. *Hydrocynus* Weberian apparatus is like that described by Weitzman (1962) in *Brycon meeki* but the tripus is fan-shaped in lateral view, (not triangular) and the neural complex is crescentic (Fig. 17).

The other abdominal vertebrae have a large neural spine. The *neural prezygapophysis* of the 5th vertebra is a thick, nub-like process, whereas those of the 6th to 11th vertebrae are elongate processes. The neural prezygapophysis of the 12th and all successive vertebrae, including the caudal elements, is a short, thumb-like process.

The *neural postzygapophyses* are short, triangular processes on both abdominal and caudal vertebrae.

Parapophyses are present on the 6th to 20th abdominal vertebrae. Each parapophysis supports a scimitar-shaped *pleural rib* in a posterior notch.

The *pleural ribs* are scimitar-shaped and each is supported dorsally by its respective lateral parapophyses up to and including the 20th vertebra.

The transitional development of the haemal arch and spine occurs between the 21st and 31st vertebrae (Fig. 18A–C), associated with which are 11 pairs of fine, elongate pleural ribs (Fig. 19) articulating with the posteroventral surface of the haemal process.

The 32nd and subsequent vertebrae are the caudal vertebrae, each with a fully developed haemal arch and spine.

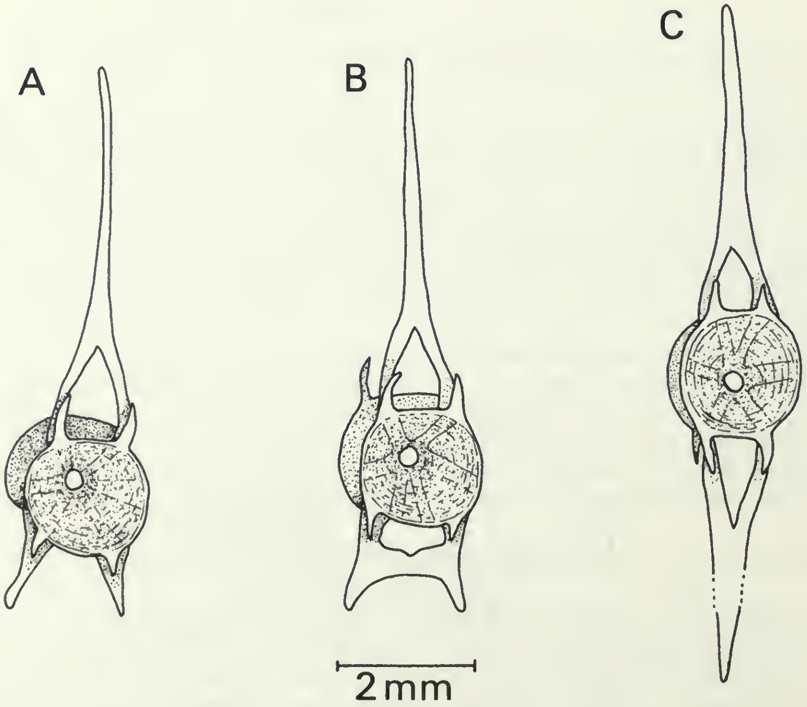


Fig. 18 *Hydrocynus forskahlii* transitional development of the haemal arch and spine. Vertebrae in anterior view. A, 21st vertebra showing haemal processes; B, 25th vertebra, the haemal processes form the canal but are bifurcate ventrally. C, 35th vertebra showing fully developed haemal spine.

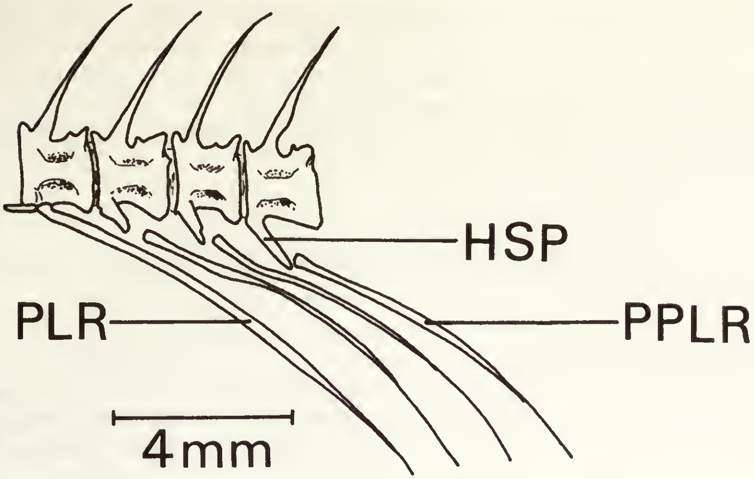


Fig. 19 *Hydrocynus forskahlii* 20th–23rd vertebrae, left side, lateral view.

Epineural and epipleural ribs

There are 44 pairs of *epineural ribs,* all of which are posterodorsally directed and forked proximally.

There are 27 pairs of *epipleural ribs,* all of which project posteroventrally; apart from the first and last pair, all are forked. The epipleurals lie lateral to the last 15 pleural ribs and the series continues posteriorly to the base of the caudal fin.

Caudal fin

Sexual dimorphism is exhibited in the *caudal fin skeleton* of all species of *Hydrocynus.* In females, the neural spines on the 2nd and 3rd preural centra are of approximately the same length, with expanded anterior and posterior flanges (Fig. 20A). The neural spines of preural centra 3 and 4 of males are more elongate than in females and curve backwards over the neural spine on the 2nd preural centrum (Fig. 20B).

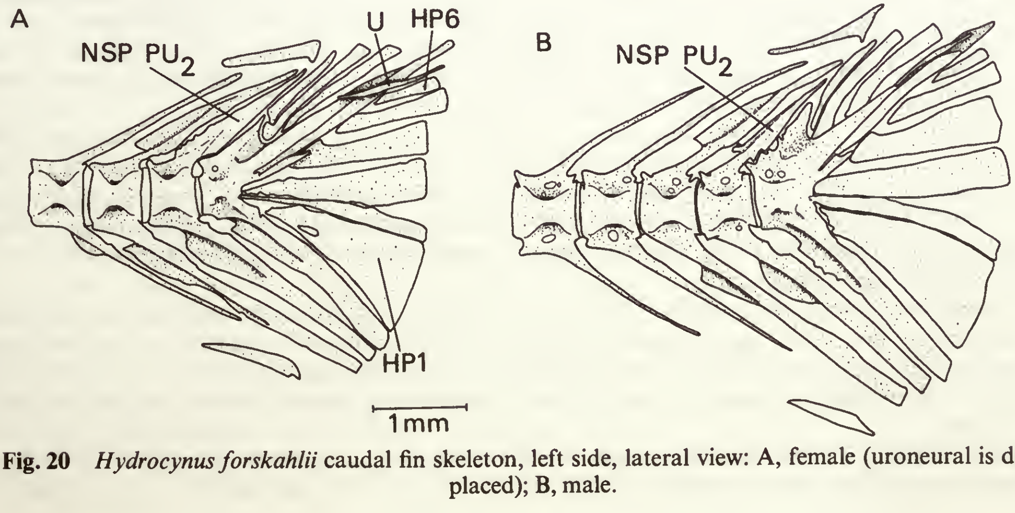


Fig. 20 *Hydrocynus forskahlii* caudal fin skeleton, left side, lateral view: A, female (uroneural is displaced); B, male.

The neural spine of the 3rd preural centrum has an expanded anterior flange in both sexes.

There are 5 autogenous *hypurals*, hypural 2 is joined to the fused $PU_1 + U_1$ centra. The adjacent margins of hypurals 1 and 2 contact each other extensively, those of hypurals 2 and 3 contact each other anteriorly, but diverge posteriorly (Fig. 20A, B).

There are two pairs of rod-shaped *uroneurals* that lie lateral to the $PU_1 + U_1$ spine and three rod-shaped epurals.

Supraneurals

There are 11 rod-shaped *supraneurals* which lie anterodorsally to the neural spines of the 4th to 14th abdominal vertebrae.

Dorsal and anal fins

The *dorsal fin* comprises 2 soft unbranched and 8 branched fin rays and their supporting pterygiophores. The *proximal radials* articulate with small, rod-shaped, *medial radials* at a cartilage interface. The anterior proximal radial has greatly expanded anterior and posterior flanges.

The medial radials articulate with the small, triangular *distal radials* at a cartilage interface.

The *anal fin* comprises 3 soft, unbranched and 12 branched fin rays and supporting pterygiophores which are similar in morphology to those described for the dorsal fin (see above).

Character analysis

On the basis of jaw and tooth structure, tooth replacement, three openings to the posttemporal fossa and the presence of a tubular orbitosphenoid process, Roberts (1966: 215; 1967: 242; 1969: 443) considered *Hydrocynus* to be related to the genus *Alestes*, stating the former 'very probably had *Alestes*-like ancestors'. Therefore, the question to be answered is whether *Hydrocynus* and *Alestes* are sister-groups, or, whether *Hydrocynus* is either most closely related to one group of *Alestes* species or some other genus currently included in the Characidae. In order to resolve this problem, the derived features of *Hydrocynus* must be established.

Those features not included in the following discussion are either dealt with later (see p. 193–201) or are symplesiomorphies for characids.

Neurocranium

The ethmoid

According to Vari (1979: 277) the plesiomorphic condition of the characiform supraethmoid process is '. . . an anteriorly triangular bone extending between, and completely or nearly completely separating the premaxillae.' Fink & Fink (1981: 306) make an alternative supposition that the absence of a distinct mesethmoid spine (supraethmoid process) and presence of a premaxillary articular fossa are primitive features for characiforms.

In *Hydrocynus*, the supraethmoid process is small and rather indistinct in comparison with other characins. It has a shallow depression in the vertical mid-line for articulation of the premaxillae (see p. 166). The Citharinidae and Distichodontidae also have a small supraethmoid process (Vari, 1979: 277–279) but since the anterior margin is modified into a trifurcate complex, it appears that reduction of the supraethmoid process has been independently derived in this lineage and *Hydrocynus*.

Contrary to the opinion of Fink & Fink (*op. cit.*) my outgroup comparison shows that a distinct triangular supraethmoid spine is present and that a premaxillary articular fossa is absent in the majority of characiforms. I therefore concur with Vari (*op. cit.*) that the presence of a triangular supraethmoid spine and absence of a premaxillary articular fossa are plesiomorphic conditions.

The lateral supraethmoid wings are primitively triangular processes, whereas in *Hydrocynus* these are blunt, thick straight processes.

The morphology of the supraethmoid process and lateral supraethmoid wings of *Hydrocynus* are autapomorphic for this genus.

Dilatator fossa and sphenotic

The posterior part of the dilatator fossa of the characiforms examined, just encroaches onto the anterior face of the pterotic. In *Hydrocynus,* the posterior part of the dilatator fossa is formed as a groove in the face of the pterotic. As this feature is not present amongst the outgroup characiforms examined, it is hypothesized to be autapomorphic for *Hydrocynus.*

The sphenotic process in *Hydrocynus* is produced laterally as a bluntly triangular shelf which slopes anteroventrally; extending medially from the process as a sharp-edged ventral strut. Examination of outgroup characiforms reveals that only *Serrasalmus* possesses a similar strut. The strut in *Serrasalmus* is perforated whereas in *Hydrocynus* the strut of bone is thick and imperforate. As in *Hydrocynus*, the lateral process in *Serrasalmus* is anteroventrally directed, but is spinous rather than shelf-like. Although the sphenotic in *Hydrocynus* and *Serrasalmus* has a generally similar morphology, there are marked differences in the shape of the spine, furthermore, in the absence of any other shared, derived features between these genera, the similarity is reasoned to be independently derived and autapomorphic for each genus.

Parasphenoid

Roberts (1969: 406) considers a straight parasphenoid to be primitive for characiforms, and the 'strongly ventrally depressed' parasphenoid characteristic of many members of the Characidae to be a specialized feature. According to Vari (1979: 288) the characiform parasphenoid is plesiomorphically a flat, straight or ventrally convex element extending posteriorly to below the basioccipital. My outgroup comparisons suggest that the parasphenoid which is markedly convex ventrally, anterior to the ascending processes (which is typical of the Characidae) appears to be the derived condition. I therefore, agree with Vari that the flat, straight parasphenoid is plesiomorphic for characiforms.

In comparison with the parasphenoid in other members of the Characidae, that of *Hydrocynus* is straight, its morphology resembling that of the plesiomorphic type.

Jaw bones

The plesiomorphic condition for the upper jaw of characiforms is immovably attached to the supraethmoid *via* large, triangular-shaped premaxillary ascending processes, which are almost entirely separated in the mid-line by the supraethmoid process (Weitzman, 1962: 32; Vari, 1979: 271 & pers. obs.) *Lepidarchus adonis* is exceptional within the Characidae in the extreme reduction of the premaxillary ascending processes and triangular supraethmoid spine. The supraethmoid region of the cranium of *L. adonis* closely resembles that of a 10 mm SL specimen of *Alestes* sp. (BMNH 1981.2.17: 1699–1734) in which the cranium is largely cartilaginous and the premaxillary ascending processes and supraethmoid spine are not yet fully developed. However, *Lepidarchus* displays reduction in many other morphological characters which suggests that reduction of the premaxillary ascending process and supraethmoid spine may be paedomorphic features.

In some *Alestes* species the premaxillae are united by a weak symphysial 'hinge' joint, comprising at the most, two interdigitating processes. The distal part of the characid premaxilla (excluding *Hydrocynus*) is tapered (Fig. 21).

The upper jaws of *Hydrocynus* (described on pp. 171–172) are seen to differ from those of other characids in the following and presumably derived features: presence of medial interdigitations along the vertical length of the premaxillae, forming a loose symphysial hinge; a short premaxillary ascending process; the distal part of the premaxilla dorso-ventrally expanded.

Another derived jaw feature in *Hydrocynus* is the presence of a double premaxillary (ethmoid) facet. The anterior facet articulates with the supraethmoid process whilst the posterior facet articulates with the lateral supraethmoid wing (see. p. 166).

Vari (1979: 271) reported the presence of a medial premaxillary articular fossa in the Distichodontidae and Citharinidae, which he hypothesized to be synapomorphic for these families.

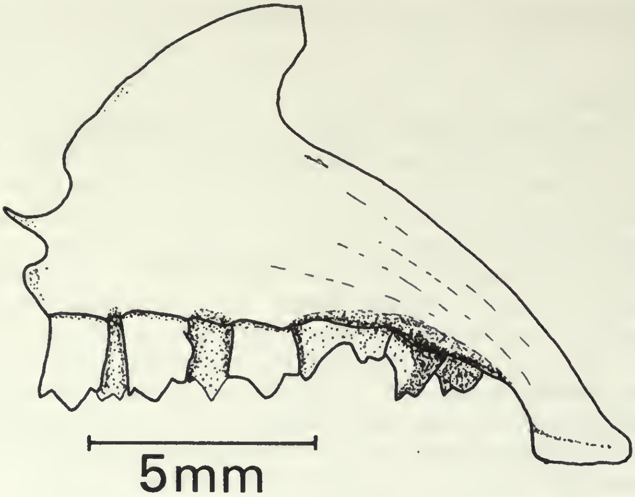


Fig. 21 *Alestes baremose* premaxilla, left side, lateral view.

However, the morphology of this socket differs from that in *Hydrocynus* in being a deep horizontal depression, open to its partner across the symphysis in *Xenocharax* (Distichodontidae). Other derived modifications of the premaxillary articular fossa amongst the citharinid-distichodontid lineage are: a conical pit; transversely directed pit, or, the fossa roof is reduced to a small shelf at the lateral margin of the depression (Vari, 1979: 271–272). The citharinids and distichodontids have a single articulation with the ethmoid rather than the double articulation of *Hydrocynus.* In view of these several differences and the absence of any other synapomorphies uniting these taxa, it is most likely that the anterior premaxillary facet of *Hydrocynus* is homoplastic with that in the Distichodontidae and Citharinidae.

The maxilla of the African characids is an edentulous comma-shaped bone, considerably thickened posteriorly. Posteromedially, the maxilla is grooved for the reception of the maxillary-mandibular ligament. In contradistinction, the maxilla of *Hydrocynus,* although edentulous, is a lamellar bone ankylosed to the premaxilla (Roberts, 1969: 415 and personal observation). In members of the neotropical characiform family Erythrinidae, the maxilla is also lamellar bone, but unlike that of *Hydrocynus*, it bears a large number of teeth and has an elongate, medially curved anterior ascending process. No other synapomorphies were found to unite these taxa, thus the apomorphous lamellar nature of the maxillae in *Hydrocynus* and the Erythrinidae is most parsimoniously explained as being independently derived.

The attachment of the maxillary-mandibular ligament to the anterolateral face of the maxilla (see p. 172) is unique to *Hydrocynus*.

The mobile articulation of the upper jaw in *Hydrocynus* is absent amongst other African characids, although found in other characiforms. Like *Hydrocynus*, the Citharinidae and some genera of Distichodontidae have a premaxillary articular fossa (see above), and lack a prominent premaxillary ascending process. The mechanism by which mobility of the upper jaw is achieved in Citharinidae and Distichodontidae is quite different from that in *Hydrocynus* (Vari, 1979: 272) and must be considered as being independently derived. A mobile premaxillary-supraethmoid articulation occurs in the neotropical characiform families Anostomidae, Chilodontidae, Prochilodontidae, Parodontidae and Hemiodontidae (Roberts, 1974; 412 & 425; Vari, 1979: 272). The morphology of the premaxillae and ethmoid region in these families is dissimilar to that of *Hydrocynus*. In the absence of any other shared, derived characters, the premaxillary mobility in these South American families appears to be non-homologous with that in *Hydrocynus*.

Dentition

Roberts (1967: 238–239) found the multicuspid teeth of characiforms to be compound elements, each cusp representing a separately formed conical element. The individual conical elements equate to a single tooth, a group of which are held together by a hard base of variable development. Roberts also thought that conical teeth are primitive for characiforms but the conical teeth of *Hydrocynus* are derived. My observations agree with those of Roberts regarding the formation of multicuspid teeth in *Alestes* and *Hydrocynus*. The tricuspid condition of *Hydrocynus* is evidently derived in each case by fusion of three 'juvenile' conical teeth and the 'adult' conical teeth are secondarily derived from the tricuspid teeth in which the median cusps are dominant (see p. 172). The juvenile conical dentition found in *Hydrocynus* and *Alestes* suggests the presence of conical teeth is the primitive condition for characiforms; the multicuspid dentition of non-juvenile *Alestes* and *Hydrocynus* of more than 23 mm SL but less than 50 mm SL is the derived condition. The conical teeth of *Hydrocynus* are considered to be secondarily derived from the tricuspid condition. This is in agreement with Roberts's hypothesis that the 'adult' conical teeth of *Hydrocynus* are derived.

The teeth of the Characidae are usually tightly bunched and contact one another in the anterior part of the relatively short jaws. In *Hydrocynus* the teeth are few in number, and are widely and evenly distributed along elongate jaws (see p. 171). Elongate jaws are characteristic of a number of supposedly primitive characiform genera, such as *Hepsetus, Ctenolucius, Salminus, Hoplias* and *Acestrorhynchus,* but with the exception of *Hydrocynus* and *Acestrorhynchus,* the teeth of these taxa are numerous, usually contiguous and are uniserial. The teeth of *Acestrorhynchus* are more numerous than in *Hydrocynus* and have large, irregularly situated diastemata.

Roberts (1969: 439) considered wide spacing of jaw teeth to have resulted from secondary elongation of the jaws. Apart from the wide spacing of the jaw teeth of *Hydrocynus*, there is no other morphological evidence to suggest that the jaws in this taxon are secondarily elongate, or indeed that this is the derived condition.

The conical 'juvenile' dentition as found in *Hydrocynus* is hypothesized to be plesiomorphic for characiforms (see above). Apparently such conical 'juvenile' teeth are the first to develop from the embryonic dental lamina, which is continuous, so that the emergent teeth all contact one another. In specimens of *Hydrocynus* larger than 16 mm SL, the dental lamina appears to be in regular, discrete units that each produce 3 tooth buds; these fuse as the tooth develops and form a tricuspid tooth.

Contra Roberts (1969: 439), I consider the wide, even spacing of the teeth of *Hydrocynus* to be the primary derived condition and not a result of secondary elongation of the jaws. Such wide, even spacing of the teeth was not found in any other characiform examined and is considered to be autapomorphic for *Hydrocynus*.

Roberts (1966, 1967) dealt with characiform tooth replacement in some detail. He described the replacement trenches of *Hydrocynus* as '. . . roofed over but . . . pierced by large foramina for each of the replacement teeth . . . ' For the reason given on p. 171 I have referred to these trenches as 'replacement cavities'. The replacement cavities are most probably derived from a single trench because the posterior cavity contains two or more replacement teeth. Roberts (1967: 233) described the replacement trenches of five genera of African characids as greatly excavated in the lower jaw, with the replacement teeth lying considerably below the bases of the corresponding functional teeth. The replacement teeth of *Hydrocynus* lie horizontally, with their tips projecting posteriorly through the cavities. The replacement teeth are also horizontally aligned in the replacement trenches of the supposedly primitive characiforms *Hepsetus* and members of the Cynodontini, however, the knowledge of distribution of this character within the characiforms is such that no polarity can be assigned to this character.

Teeth are replaced on alternate sides of the jaw in *Alestes* species, but in several specimens of *Hydrocynus* that are in the process of replacing teeth, the entire functional dentition is lost simultaneously. In the jaws of a specimen of 25 mm SL (BMNH 1981.2.17: 2600–2609) in the process of replacing teeth, the bone of the dentary surrounding the functional teeth and replacement cavities has been resorbed. The complete loss of the functional dentition is reported by

Begg (1973) who noted high proportions of toothless *Hydrocynus* being caught by anglers. The stomach contents of some of these specimens included shed teeth, so it is assumed the teeth are often swallowed. Begg kept eight tigerfish in captivity for a month and found dozens of teeth on the floor of the tank at the end of this period; he presumed that all the fish had shed their teeth and successfully replaced them. Tweddle (1982) also reported the complete loss of functional dentition in a species he called *Hydrocynus vittatus*. Roberts (1967: 238) reported only *Schizodon fasciatus* (Characiformes: Anostomidae) as losing and replacing its entire dentition in one stage. Too few data are available on the occurrence of complete *vs* incomplete tooth loss amongst characiforms for any polarity assignment to be given to these characters.

Circumorbital bones

Roberts (1969: 419) considers the characiform series to be primitively comprised of eight bones: a supraorbital, antorbital and six infraorbitals. All characids examined for outgroup comparison in this study have a circumorbital series comprising these eight bones as follows and as exemplified by *Alestes dentex*:

The antorbital is spear-shaped (Fig. 22) and tightly bound by connective tissue to the anterolateral margin of the frontal; it lies anterior to the supraorbital and the posterodorsal margin of the first infraorbital; the first infraorbital, or lachrymal is narrow and rectangular, and lies lateral to the ascending process of the maxilla; the second infraorbital is of similar shape, but lies posterior to the maxilla; the third, fourth and fifth infraorbital bones are large, cover the cheek, and are similar to those described for *Hydrocynus* (see p. 173); the dermosphenotic is a rectangular bone with an anterodorsal process, and is bound by connective tissue to the lateral edge of the frontal and to the posterior part of the supraorbital; the supraorbital is an elongate, thick, rod-like bone lying anterior to the dermosphenotic; it contacts the lateral edge of the frontal and the antorbital anteriorly.

The laterosensory canal runs along the orbital margin of the circumorbital series and bifurcates in the dermosphenotic, as described for *Hydrocynus* (see p. 173).

The first infraorbital of *Hydrocynus* is a broad bone relative to that in other characiforms, and lies lateral to the premaxilla as well as the ascending limb of the maxilla. The second infraorbital is also greatly enlarged, concealing most of the maxilla. Such enlargement of the first and second infraorbital bones is unique to *Hydrocynus*.

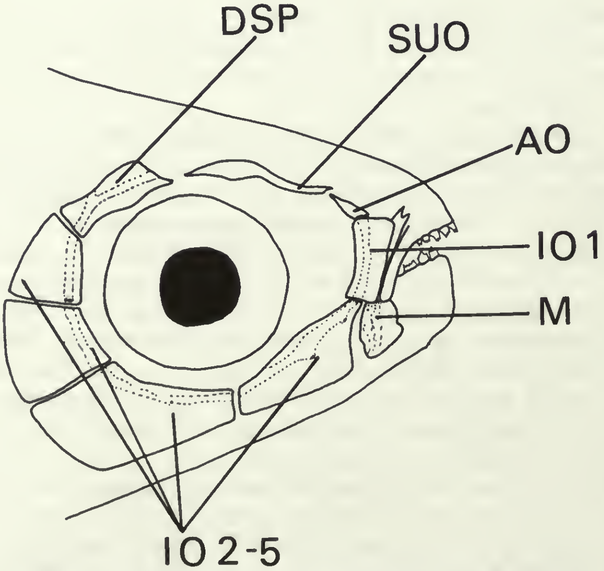


Fig. 22 *Alestes dentex* circumorbital series, right side.

Suspensorium

The hyomandibula of *Hydrocynus* is similar to that of other characiforms except for the presence of a dorsolateral spine (see p. 174). As this spine is not found in any other outgroup characiform examined, it is recognized as autapomorphic for *Hydrocynus*. Amongst other teleosts, there is a process on the posterolateral surface of the hyomandibula in the Clupeidae. This process projects as an anteriorly directed flange along the length of the hyomandibular shaft, and is unlike that found in *Hydrocynus*. In the absence of any synapomorphies suggesting a relationship between these taxa, the hyomandibular spine of *Hydrocynus* and hyomandibular process in the Clupeidae are proposed to be independently derived.

The modal (and presumably plesiomorphic) condition for the ectopterygoid in characiforms is an elongate, ovate, toothed bone which contacts the quadrate ventrally and extends along the anterior margin of the endopterygoid. The shortened, disc-like ectopterygoid of *Hydrocynus* was not found in any other characiform examined and is hypothesized to be autapomorphic for *Hydrocynus*. Roberts (1969: 418) states that the presence of ectopterygoid teeth in characiforms has a mosaic distribution. However, none of the African characids that I examined possess ectopterygoid teeth (see also p. 203).

Interrelationships of *Hydrocynus*

From the above analysis, the following apomorphic characters have been identified for *Hydrocynus*, and will form the basis of a discussion concerning the interrelationships of the genus.

1. Supraethmoid process small but specialized with a shallow depression for articulation of the premaxillae. The supraethmoid of other characiforms is usually large and triangular, separating the premaxillae.
2. Supraethmoid wings blunt, thick, straight processes. The supraethmoid wings of outgroup characiforms are plesiomorphically small triangular processes.
3. Pterotic grooved posteriorly, such a groove is absent in all other characiforms examined.
4. Sphenotic with a ventromedial strut, which with the exception of *Serrasalmus* (see p. 185) is absent in all other characiforms.
5. Upper jaw articulates with the supraethmoid. With the exception of the Citharinidae and Distichodontidae (see p. 186), the upper jaw of characiforms is immovably attached to the supraethmoid.
6. Premaxillae with synarthritic connection, such a connection is absent in other characiforms.
7. Premaxillary ascending processes short, which in other characiforms are present as large triangular processes.
8. Premaxilla deepened distally. The distal part of the premaxilla in other characiforms is tapered.
9. Premaxillary facet present. This facet is absent in other characiforms with the exception of the Distichodontidae and the Citharinidae (see p. 186).
10. Premaxillary dorsomedial facet present, this facet was not found in any other characiform examined.
11. Maxilla lamellar, edentate and ankylosed to premaxilla, whereas the maxilla of other characiforms is comma-shaped and thickened posteriorly, with the exception of the Erythrinidae (see p. 186).
12. Maxillary-mandibular ligament attached to anterolateral face of maxilla. In other characiforms this ligament is attached to the posteromedial surface of the maxilla.
13. Tooth replacement cavities present, as opposed to the open trenches found in other characiforms.
14. Conical teeth, secondarily derived from a tricuspid condition. The teeth of other characids are multicuspid.
15. Teeth widely and evenly spaced. In other characiforms, the teeth are usually contiguous, or have irregularly situated diastemata.

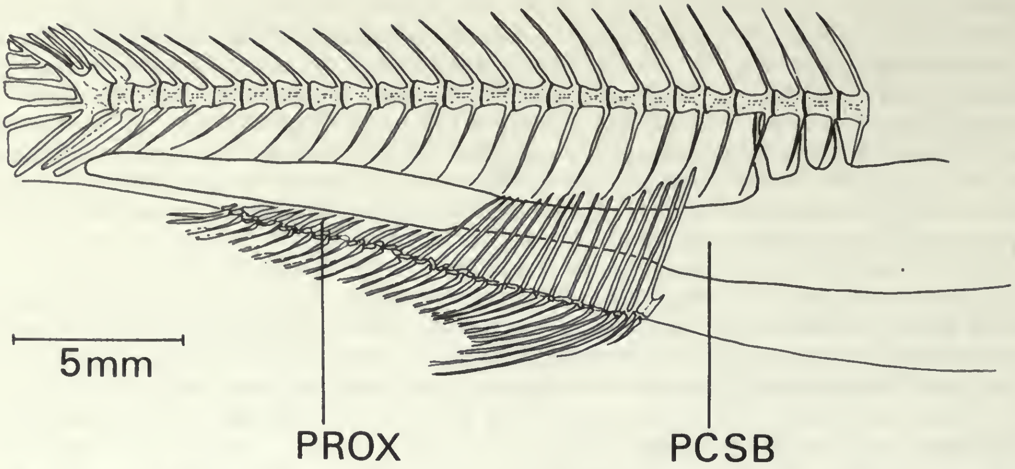


Fig. 23 *Alestes dentex* anal fin, posterior portion of vertebral column and swimbladder, right side, lateral view.

16. 1st and 2nd infraorbital bones enlarged, in other characiforms these are both narrow and rectangular, with the latter lying posterior to the maxilla.
17. Hyomandibular spine present. No such spine occurs in any other characiform.
18. Ectopterygoid reduced in length. The ectopterygoid of other characiforms is an elongate, ovate bone.

Roberts (1966, 1967 & 1969) suggested that *Hydrocynus* was derived from an *Alestes*-like ancestor, interpreting *Alestes* in the sense used by Boulenger (1907). Myers (1929), Poll (1976) and Géry (1968: 1977) recognizing that Boulenger's *'Alestes'* is polyphyletic have, however, reinstated the genera *Brycinus* Cuvier & Valenciennes 1849 and *Myletes* Peters 1852, taxa which Boulenger incorporated in his concept of *Alestes*. My continuing studies on the osteology of '*Alestes*' (*sensu* Boulenger) tend to confirm the opinions of Myers, Poll and Géry, that it incorporates at least three taxa each of which has closer relatives with species in other genera and furthermore, that one of these is more closely related to *Hydrocynus* than are the others. This latter group of species, which, pending a revision of the genus, is referred to as *Alestes sensu stricto,* includes the species: *dentex* (type species of the genus), *baremose, ansorgii, macrophthalmus, stuhlmanni* and *liebrechtsii.* It is characterized by the two following apomorphies:

19. Posterior chamber of the swimbladder extends to the haemal spine of the third preural centrum (Fig. 23). In all other species of '*Alestes*' and other outgroup characiforms examined, the swimbladder extends to the origin of the anal fin.
20. The posterior proximal radials of the anal fin are short and curved anteriorly (Fig. 23). These radials in the anal fin of all other '*Alestes*' species, and other characiforms examined, are straight, aligned anterodorsally and not conspicuously shortened.

Those characters which are thought to be synapomorphic features uniting *Alestes s.s.* with *Hydrocynus* are considered below, and will be compared with those in remaining species in *Alestes sensu lato,* and other characiform taxa.

Dilatator fossa and sphenotic process

According to Vari (1979: 317, 319 & 326) and Howes (1981: 15) the plesiomorphic characiform dilatator fossa is small, is formed by almost equal contributions from the frontal, sphenotic and pterotic and is roofed or partially roofed by the frontal. This form of the dilatator fossa is Type 1 *sensu* Howes (1978: 56). In *Hydrocynus, Alestes s.s.* and *Oligosarcus*, the fossa is long and deep, with an extensive frontal contribution. It approximates to Type 2 *sensu* Howes (1978: 56).

The anterior margin of the dilatator fossa is formed by the sphenotic process, which in *Hydrocynus* and *Alestes s.s.* is thick and ventrally directed (see below) so that the fossa is broad in lateral view. In *Oligosarcus,* the sphenotic process is thin, sickle-shaped and directed backwards, thus the fossa is narrow in lateral aspect. Although the dilatator fossae of *Hydrocynus, Alestes s.s.* and *Oligosarcus* are long and deep, there are differences in the way the sphenotic, frontal and pterotic contribute to them, indicative of their independent derivation. Thus, the long, deep dilatator fossa shared by *Hydrocynus* and *Alestes s.s.* is thought to be synapomorphic for these genera.

The sphenotic process of characiforms is thin and directed ventrally forming part of the posterior wall of the orbit. In *Hydrocynus* and *Alestes s.s.* the process is well-developed and thickened ventrally. A similar form of the sphenotic process was not found in any other characiform examined, and thus is considered a derived feature shared by *Hydrocynus* and *Alestes s.s.*

Parasphenoid

In the absence of any synapomorphies indicating that *Hydrocynus* is more closely related to any characiform taxon outside the Characidae, the straight parasphenoid characteristic of this genus is most parsimoniously explained as homoplastic with that of other characiform taxa sharing this feature.

Pleural ribs

All species of *Hydrocynus* have 10 or 11 pairs of fine, elongate pleural ribs that articulate with the posteroventral surface of the haemal process and are associated with the transitional development of the haemal arch and spine between the 21st, or 22nd and 31st vertebrae, (see p. 182). In *Alestes s.s.* the counts are: *ansorgii*, *baremose*, *macrophthalmus* 8; *stuhlmanni* 9; *dentex* 10–11; *liebrechtsii* 10–11. The counts for *Alestes s.l.* are: *minutus*, *stolatus* 2; *lateralis*, *longipinnis* 3; *carolinae*, *tholloni*, *dageti*, *leuciscus* 4; *nurse*, *jacksoni*, *opisthotaenia*, *senegalensis* 5; *nigricauda*, *sadleri*, *poptae*, *lemairii*, *grandisquamis*, *macrolepidotus* 6.

In other characiforms, there are also pleural ribs articulating with the posteroventral surface of the haemal process. Counts on those taxa examined are: *Charax* 2; *Rhabdalestes*, *Bryconaethiops* 2–3; *Brycon*, *Triportheus*, *Scissor*, *Lebiasina* 3; *Acestrorhynchus* 4; *Hydrolicus* 5; and *Hepsetus* 6. Exceptionally, *Lepidarchus* does not have any pleural ribs articulating with the posteroventral surface of the haemal process.

On the basis of those outgroup comparisons within the Characiformes the higher number of 8 or more paired 'posterior pleural' ribs occurring in *Hydrocynus* and *Alestes s.s.* seem to represent the derived condition and is considered to be synapomorphic for these taxa.

Orbitosphenoid tube

Starks (1926: 167) described a bony orbitosphenoid process surrounding the olfactory tract and bulb in *Alestes liebrechtsii* and *A. grandisquamis*. Roberts (1969: 441) also observed this process in *Alestes baremose*, *A. imberi*, *A. macrolepidotus*, *Bryconaethiops* and *Hydrocynus* (see p. 170). Vari (1979: 341) added *Alestes dentex* and *A. macrophthalmus* to those taxa listed above, and suggested that a tubular orbitosphenoid process is an apomorphy shared by these taxa. Although Weitzman (1962: 20) and Howes (pers. comm.) noticed that *Brycon* also has a bony tubular process that encases the olfactory nerve, this is a process developed from the lateral ethmoid and not a homologue of the tube under discussion.

In addition to those taxa mentioned, the following also share this feature: *Alestes sensu stricto*; *A. nurse*; *A. grandisquamis*; *A. macrolepidotus* and *A. jacksoni*. It seems the tubular orbitosphenoid process is either apomorphic for this lineage, or, that this feature has a mosaic distribution in the African Characidae. However, pending a revision of the genus *'Alestes'* no polarity can be assigned to this character.

Caudal neural spines

Sexual dimorphism in the neural spine morphology of preural vertebrae 1 and 2 as seen in *Hydrocynus* (see p. 183), occurs in all members of the African Characidae examined, except for *Lepidarchus*. Vari (1982, p. 4), describes dimorphism in the neural spines of preural vertebrae 2 and 3 in the neotropical genus *Curimatopsis* (Curimatidae). Here, the neural spines in males have greatly expanded anterior and posterior flanges, a condition unlike that in the males of African characid species which have a reduced neural spine on preural 2 and elongate, curved neural spines on preurals 3 and 4. This difference, together with the absence of any other shared, derived features, and furthermore since Vari (1983: 46) lists a series of characters indicating curimatids are related to the Neotropical family, Prochilodontidae, suggests this form of sexual dimorphism has been independently derived in the two groups.

On the basis of the above analysis, the following characters are proposed as synapomorphies for *Hydrocynus* and *Alestes s.s.*, which taxa are thus considered to be sister-groups (see Fig. 24):

21. long, deep dilatator fossa;
22. well-developed, ventrally thickened sphenotic process;
23. 8–11 pairs of fine, elongate pleural ribs articulating with the posteroventral surface of the haemal process.

Géry (1968) studied the classification of '*Alestes*', (including *Bryconaethiops microstoma*), utilizing numerical taxonomy to analyse data obtained from a number of morphometric, meristic and colour features. His results, produced as a phenogram, show the group of characids referred to here as *Alestes s.s.* to be more closely related to *Bryconaethiops* than either genus is to any other species or group of species included in *Alestes sensu lato*. Géry's hypothesis that *Alestes s.s.* and *Bryconaethiops* are sister-groups is in contradiction to the relationship between *Alestes s.s.* and *Hydrocynus* proposed here. I have been unable to detect any osteological characters to

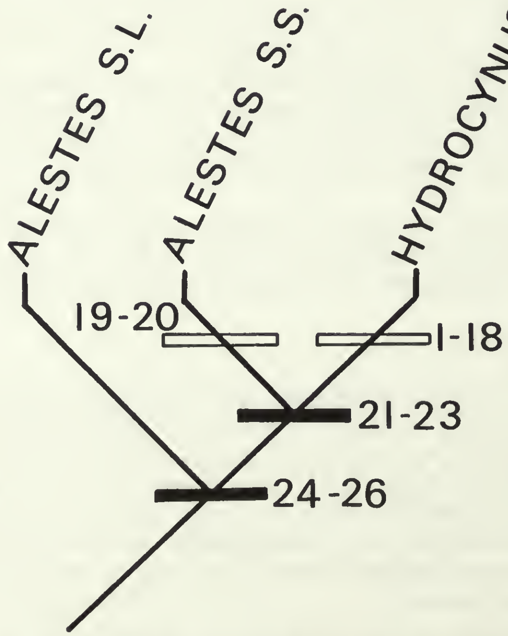


Fig. 24 Synapomorphy diagram of relationship between *Hydrocynus*, *Alestes s.s.* and *Alestes s.l.* Open bars indicate autapomorphies, black bars indicate synapomorphies, numbers 24–26 are as follows: (24) unique upper jaw morphology; (25) absence of ectopterygoid teeth; (26) sexual dimorphism exhibited in the posterior neural spines (see p. 183).

support Géry's findings and consider *Bryconaethiops* to be more closely related to some other '*Alestes*' lineage than to either *Alestes s.s.* or *Hydrocynus.*

The proposed relationship of *Hydrocynus* and *Alestes s.s.* is discussed further on pp. 202.

Revision of *Hydrocynus* species

As stated earlier (see p. 164), there is some confusion regarding the validity of certain nominal species of *Hydrocynus.* Previous authors (Günther, 1864; Boulenger, 1901; 1907) relied on meristic characters to differentiate between species. Four species of *Hydrocynus* are recognized here, based on morphometric, meristic and osteological characters.

Hydrocynus forskahlii Cuvier (Fig. 25B)

Hydrocynus forskahlii Cuvier 1819 *Memoires du Muséum d'Histoire Naturelle* **5:** 354–357
Characinus dentex (non Lacepède) Geoffroy Saint Hilaire 1809 *Description de l'Egypte* **24:** 236–244, pl. 4
?*Hydrocynus vittatus* Castelnau 1861 *Memoire sur les Poissons de l'Afrique Australe:* 65–66
Hydrocyon lineatus (attributed to Schlegel) Bleeker, 1863 *Natuurkundige Verhandelingen van de Bataafsche Hollandsche Maatschappye der Wetenschappen te Haarlem Z. Verz.* **18:** 125

NOTE ON THE SYNONYMY. The type specimen of *Hydrocynus vittatus* Castelnau 1861 is no longer extant (Boulenger, 1907: 106). Castelnau's description is undoubtedly that of a tigerfish; he gives the collection locality as Lake Ngami (Okovango drainage, Botswana) and *H. forskahlii* is the only species known to occur in that area. It therefore seems most likely that *H. vittatus* is a synonym of *H. forskahlii.*

I have examined the type of *H. lineatus,* which is in poor condition comprising little more than the skull, caudal skeleton and skin. On the basis of morphometric and meristic data, together with radiographs of the skull, I am satisfied that *H. lineatus* is a synonym of *H. forskahlii.*

NOTE ON THE HOLOTYPE. The holotype of *H. forskahlii* is in the collections of the Muséum National d'Histoire Naturelle, Paris (MNHN 1691). In addition to this specimen, the following MNHN specimens A9705, A9708, A9707, A9709, A9710, A8548, A8607, A9711 and 1692 are listed by Bertin (1939) as part of a syntypic (*sic*) series of *H. forskahlii* and are labelled as such. I disagree that these specimens should be included in the type series for the following reasons: Specimens A9705 and A9710 were collected from the Nile by Joannis in 1834, subsequent to Cuvier's 1819 description. The following specimens were collected from Sénégal A9707 by Heudelot; A9708, A9711 by Jubelin (the latter in 1828) finally, A9709 and 1692 by Leprieur, whereas Cuvier's description gives the type locality as the Nile. Specimens A8548 and A8607 were collected from the White Nile by Darnaud in 1843.

I note that Daget *et al.* (1984: 170) state only MNHN 1691, A9705, A9707, A9708 and A9709 are syntypes.

The holotype is in poor condition, with few scales remaining on the body; the infraorbitals of the right hand side are loose and the right upper jaw is disarticulated.

DIAGNOSIS. The body of *H. forskahlii* (Fig. 25B) tends to be less deep (mean = 22·6 expressed as a percentage of the standard length) than that of its congeners, and the lateral stripes are prominent. It differs from *H. brevis* with which it is sympatric, in having slender gill rakers, which are approximately equal to the gill filaments in length.

DESCRIPTION. Based on the holotype and 175 other specimens, ranging in size from 51·2–442 mm standard length. Depth of body 17·2–27·8 (mean = 22·6) per cent of standard length, length of head 15·3–25·3 (mean = 19·8) per cent. The dorsal profile of the head is straight. Interorbital width 6·1–10·8 (mean = 7·9) per cent, width of 4th infraorbital 5·1–7·5 (mean = 6·1); snout length 6·1–10·2 (mean = 8·3) per cent; depth of premaxilla 1·7–3·9 (mean = 2·7) per cent of standard length.

Gill rakers: Long and slender, approximately as long as the gill filaments; 8–10 (mode 9) rakers on the first ceratobranchial.

Scales: Lateral line with 46 (f. 10), 47 (f. 31), 48 (f. 30), 49 (f. 26), 50 (f. 31), 51 (f. 19), 52 (f. 12) or 53 (f. 7).

Fins: Dorsal with 2 soft, unbranched rays and 8 branched rays in all specimens. Anal with 3 soft, unbranched rays and 11 (f. 6), 12 (f. 132), 13 (f. 9) or 14 (f. 1) branched rays.

Teeth: In the upper jaw caniniform, large and widely spaced anteriorly, and smaller and tricuspid posteriorly, numbering 9 (f. 2), 10 (f. 10), 11 (f. 4), 12 (f. 126), 13 (f. 4) or 14 (f. 19). Lower jaw with 8 (f. 4), 9 (f. 4), 10 (f. 56), 11 (f. 15) or 12 (f. 66) teeth, identical in morphology to those of the upper jaw. Of those specimens with 14 upper jaw teeth, 16 are from coastal flowing rivers in Liberia and Ivory Coast and 3 are from L. Rudolf. This difference in tooth number appears to be a populational variation as there is no osteological or other evidence to suggest these specimens are not *H. forskahlii*.

Vertebrae: 45–51, counted as abdominal + caudal elements: 28+16 (f. 1); 28+17 (f. 2); 28+18 (f. 4); 29+16 (f. 1); 29+17 (f. 12); 29+18 (f. 1); 30+17 (f. 6); 30+18 (f. 1); 32+18 (f. 6) or 32+19 (f. 1).

Osteology: Hydrocynus forskahlii differs from its congeners in the following osteological features:

The lateral ethmoid wing is dorsally thickened and sickle-shaped in lateral view (Fig. 1B). In the other *Hydrocynus* species, it is narrow and crescentic in shape.

In the region of the dilatator fossa, the frontal is produced as a lip that partially roofs the fossa. In *H. brevis* the dilatator fossa is extensively roofed by the frontal (see p. 196) and in *H. goliath* and *H. tanzaniae,* the dilator fossa is unroofed.

DISTRIBUTION. Nilotic drainage; Senegal, Guinea, Sierra Leone; Liberia, Ivory Coast, Ghana, Nigeria, Cameroun, Zaire drainage, Zambesi drainage including L. Malawi, Limpopo, the Pongolo River system, Okovango basin, L. Ngami and as far south as L. Sibaya N. Natal.

MATERIAL EXAMINED. Holotype: MNHN 1691, River Nile; BMNH: 1937.4.20: 1–6, L. Gandjule, Ethiopia; 1907.12.2: 481–486, Nile, Beni Suef, Egypt; 1907.12.2: 511–519, Nile, Luxor and Aswan; 1949.10.20: 22–23, R. Volta; 1905.7.25: 79–80, L. Gandjule, Ethiopia; 1953.4.28: 129–130, Ogun R. Nigeria; 1953.4.28: 129–130, Ogun R. Nigeria; 1907.12.2: 487, Sanhur R. Nile; 1907.12.2: 526, Upper Nile, Korosko; 1907.12.2: 537, Mouth of L. No, White Nile; 1907.12.2: 527–528, Ibrim, Upper Nile; 1907.12.2: 474, L. Edkon; 1907.12.2: 524, Abu Hoor, Upper Nile; 1899.8.23: 58–59, Niger; 1934.8.31: 36, Volta, Ashanti Forest; 1904.1.19: 5, Tsutyaba, Albert Nile; 1932.6.13: 25–34, L. Rudolf; 1976.11.12: 52–58, Little Scarcies R., Sierra Leone; 1932.12.16: 39, Luangwa Valley; 1929.1.24: 60, Victoria Nile; 1907.12.2: 541–544, Mouth of L. No, Nile; 1907.12.2: 545–547, Gondokoro, (Sudan) Nile; 1943.7.27: 169–171, R. Chambezi and Bangwelu Swamps; 1899.9.26: 74, Leopoldville, Congo (Kinshasa, Zaire); 1908.11.6: 6–12 Upper Zambezi, above Victoria Falls; 1977.6.27: 275–298; L. Sibaya, N. Natal; 1975.6.20: 62, Luhra, Zaire; 1975.6.29: 59–60, L. Tomphwe, Zaire; 1975.6.20: 65, Ituri Bridge, Zaire; 1969.3.25: 38, Sokoto R. Nigeria; 1978.12.5:2–3 Manantali Dam Site, Senegal; 1975.6.20: 66 Luhra, Zaire; 1975.6.20: 67, Lukuga R. Zaire; 1981.2.17: 1258–1259, L. Rudolf (Turkana); 1932.6.13: 25–34, L. Rudolf (Turkana); 1903.4.24: 181, R. Offin; 1981.2.17: 590–591, L. Rudolf (Turkana); 1907.12.2: 3738 Nile; 1864.5.3: 1, R. Shire; MRAC 79.1.P. 362, L. Upemba, Belgian Congo (Zaire); 78.6.P. 463–464, R. Cuango, Angola; 183706–183707, Kariba Lake, Rhodesia (Zimbabwe); 79.1.P. 1361, Lufira, Belgian Congo (Zaire); 82.13.P. 1223–1226, R. Oubangui, Central African Republic; 183708–710, Sanyati R., Rhodesia (Zimbabwe); 166415–416, Ubangi R., Belgian Congo (Zaire); 158580, Dundo, Angola; 158581, R. Karai, Angola; 78.14.P. 127, Gorom R., Senegal; 189342, Wilia, Zaire; 76.14.P. 607–610, Koum, Cameroun; 154071–073 Fort Archambault, Tchad; 73.26.P. 40, Karaska, Tchad; 179926, Dungu R., Belgian Congo (Zaire); 76.14.P. 889–890 Mieri R., Doume, Cameroun; 73.10.P. 981–982, Toyebli, R. Cerr, Ivory Coast; 73.12.P. 81–83, Mopti, S. Mali; 73.12.P. 85, Mopti, S. Mali; 73.14.P. 53–54, Ogbone, Mono R., Togo; 82.28.P. 150–152, L. Abaya, Ethiopia; 73.12.P. 84, Mopti, S. Mali; 73.7.P. 28 Kete Krachi, Ghana; 73.5.P. 481, R. Ouime, Whedda, Dahomey; 73.10.P. 993–994, Mano R., Liberia; 73.10.P. 908 Toyebli, R. Cerr, Ivory Coast; 73.7.P. 29 Yetji, Ghana; 73.18.P. 776–782, Lagdo, R. Benoue, Cameroun; 73.15.P. 323–326, Garoua, R. Benoue, Cameroun; 73.10.P. 996–997, St Paul R., Mt Coffee, Liberia; 74.14.P. 291, L. Kossou, Ivory Coast; 74.14.P. 289–290, L. Kossou, Ivory Coast; 74.14.P. 2712, L. Kossou, Ivory Coast; 73.10.P. 998–1003, St Paul R., Mt Coffee, Liberia; 74.14.P. 2895–2802, L. Kossou, Ivory Coast; 80.19.P. 44, Sassandra R., Ivory Coast; 80.36.P. 816, Liberia; RMNH: 3279 (holotype of *Hydrocyon lineatus*) Ashantee, Guinea; MRHN: 8892, Rhodesia (Zimbabwe); 7539, Stanleyville (Kisangani, Zaire).

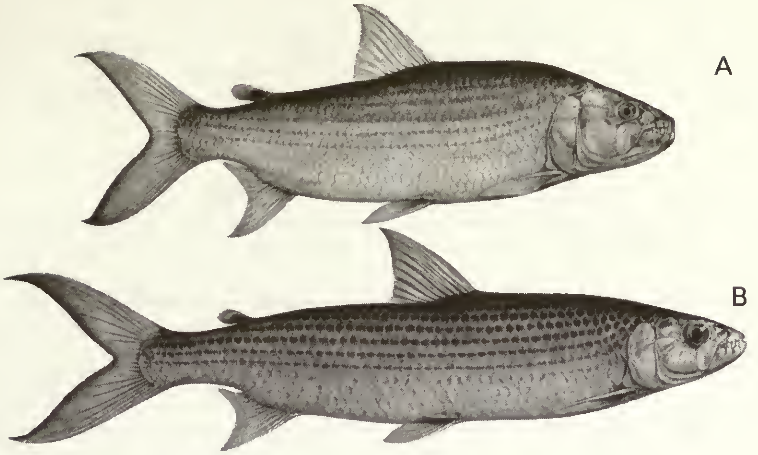


Fig. 25 A, *Hydrocynus brevis;* B, *Hydrocynus forskahlii* (taken from Boulenger 1907 *The fishes of the Nile.* Plate xv).

Hydrocynus brevis Günther
(Fig 25A)

Hydrocynus brevis Günther 1864 *Catalogue of Fishes* **5:** 351
?*Hydrocynus somonorum* Daget 1954 *Memoires de l'I. F. A. N.* no. 36: 116–117.

Lectotype. Günther's description is based on three females in the collections of the BMNH. A specimen of 247 mm standard length, from Khartoum (BMNH 1862.6.17: 94) is designated here as the lectotype. The remaining two specimens, of 232 mm and 275 mm standard length (BMNH 1862.6.17: 95–96) thus become paralectotypes.

Note on the synonymy. The types of *H. somonorum* are no longer extant (M. L. Bauchot, pers. comm.). I have examined the single non-type specimen labelled as *H. somonorum* and am satisfied this is a specimen of *H. brevis*. Daget's description of *H. somonorum* agrees with that of *H. brevis*, and he comments on the close resemblance of the two nominal forms but considers them distinct species on the basis of the short head; very small eye; position of the dorsal fin; number of scales above and below the lateral line and the fewer vertebrae in *H. somonorum*. I find Daget's morphometric and meristic data for the types of *H. somonorum* lie within the ranges of those of *H. brevis*.

Diagnosis. *Hydrocynus brevis* has a deeper body (mean = 24·4 per cent of the standard length) than the other species. The lateral stripes are less conspicuous than those of either *H. forskahlii* or *H. tanzaniae*. The infraorbital width is greater in this species (mean = 7·7 per cent of the standard length) and the gill rakers are short, approximating to one third the length of the gill filaments.

Description. Based on the lectotype 247 mm SL., paralectotypes 232; 275 mm SL and 83 other specimens, ranging from 41·3–442 mm SL. Depth of body 19·1–29·6 (mean = 24·4) per cent of standard length, length of head 18·5–24·5 (mean = 21·3) per cent. The dorsal profile of the head is straight to the posterior margin of the parietals, the supraoccipital is slightly crested. Interorbital width 8·0–10·3 (mean = 9·2) per cent; 4th infraorbital width 6·9–8·9 (mean = 7·7) per cent; snout length 8·1–13·8 (mean = 10·0) per cent; depth of premaxilla 3·0–5·3 (mean = 3·8) per cent of standard length.

Gill rakers: Short, approximately one third the length of the gill filaments, 7–10 (mode 8) rakers on the first ceratobranchial.

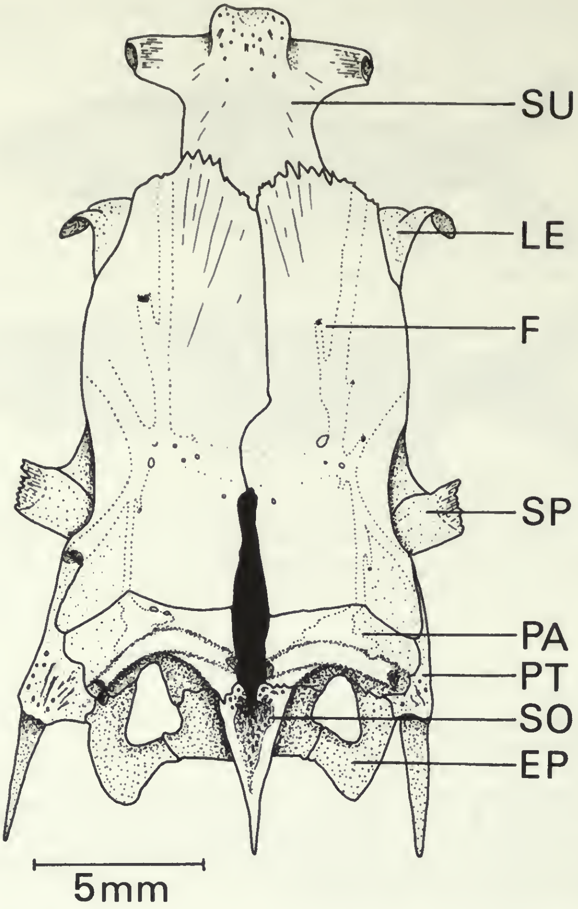


Fig. 26 *Hydrocynus brevis* neurocranium, dorsal view.

Scales: Lateral line with 47 (f. 2), 48 (f. 2), 49 (f. 11), 50 (f. 22), 51 (f. 21), 52 (f. 13), 53 (f. 11), 54 (f. 2) or 55 (f. 1) scales.
Fins: Dorsal with 2 soft unbranched and 8 branched rays in all specimens. Anal with 3 soft unbranched rays and 11 (f. 4), 12 (f. 61) or 13 (f. 16) branched rays.
Teeth: Are like those described for *H. forskahlii,* with 10 (f. 27), 11 (f. 2) or 12 (f. 55) in the upper jaw and 8 (f. 7), 10 (f. 51), 11 (f. 3), 12 (f. 22) or 13 (f. 1) in the lower jaw.
Vertebrae: 49–51; counted as abdominal + caudal elements: 31 + 18 (f. 6), 31 + 19 (f. 3), 32 + 16 (f. 1); 32 + 18 (f. 3).
Osteology: The osteology of *H. brevis* differs from that of *H. forskahlii* in the following features: The region of the frontals which roofs the dilatator fossa is produced as a thin, flat ledge of bone (Fig. 26), this region of the frontals in *H. forskahlii* partially overlaps the medial border of the fossa, whilst in *H. goliath* and *H. tanzaniae* the fossa is not overlapped by the frontals (Fig. 28 & 31).

The sphenotic process is very short and peg-like in contrast to the other species of *Hydrocynus* which have a well-developed, ventrally thickened process.

DISTRIBUTION. Nilo-Sudan, Upper Guinea, Cameroun, Togo, Ghana and Ivory Coast.

MATERIAL EXAMINED. BMNH: lectotype 1862.6.17: 94, Khartoum; paralectotypes 1862.6.17: 95–96, Khartoum; 1907.12.2: 3768–3776, nr. Luxor; 1982.4.13: 744, Sokoto R., Nigeria; 1949.10.20: 24, Dasikope, Gold Coast (Ghana); 1905.3.15: 6, Shari R.; 1907.12.2: 559–573, nr. Luxor; 1900.6.28: 77, Matam, Senegal; 1907.12.2: 549–558, nr. Luxor; 1862.9.19: 10 Nile; MNHN: A8548, White Nile; A8607, White Nile; A9710, Nile; A9711, Senegal; 1692, Senegal. MRAC: 78.14.P. 34–36, Mbane, Senegal; 73.13.P. 57–58, R. Ori, Togo; 73.12.P. 89–91, Mopti, S. Male; 73.15.P. 307–311, Waga, Cameroun; 75.5.P. 491, Doropo, Ivory Coast; 73.12.P. 87–88, Mopti, S. Mali; 73.7.P. 30–31, Kete Krachi, Ghana; 73.15.P. 312–313, Waga, Cameroun; 73.26.P. 41–43, Tchad; 73.26.P. 44–45, Tchad; 82.28.P. 37, Nile; 75.66.P. 1, Siquiri, Guinea; 70.2.P. 178–181, Gambia R. Senegal; 73.13.P. 55–56, San Sargon R., Togo; 79.2.P. 171–177, Mbane, Senegal.

Hydrocynus goliath Boulenger
(Fig. 27)

Hydrocynus goliath Boulenger 1898 *Annales du Musée du Congo Belge. Zoology* **1:** 23, plate xi.

Hydrocynus vittatus (non Castelnau) Boulenger 1898 *Annales du Musée du Congo Belge. Zoology* **1:** 24, plate x, fig. 2.

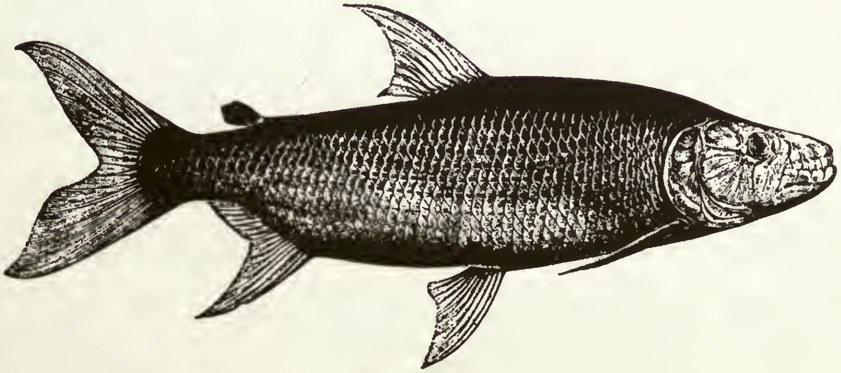
Hydrocynus vittiger Boulenger 1907 *Zoology of Egypt: The Fishes of the Nile.* Egyptian Government Publishers; as a footnote on p. 106.

NOTE ON THE SYNONYMY. Boulenger described both *H. goliath* and *H. vittiger* from specimens collected in the Zaire river system. He distinguished them on morphometric and meristic characters, in which there is some overlap. In his description, Boulenger stated *H. vittiger* had only 10 upper jaw teeth, but the types have at least two additional teeth on each premaxilla at the rictus of the jaws, which Boulenger failed to notice. Since the osteology and external morphology of the two species are identical, I consider *H. vittiger* a junior synonym of *H. goliath.* The latter name has precedence because *H. vittatus* Boulenger 1898 was invalid as it was preoccupied by *H. vittatus* Castelnau 1861; also according to Daget *et al.* (1984: 171–172) it has been more widely used.

LECTOTYPE. Of the six original specimens described, two were deposited in the collections of the BMNH and four in the MRAC, Tervuren. One of the specimens in the BMNH, collected by Captain Wilverth from New Antwerp, cannot be traced. The other, a female of 672 mm standard length (BMNH 1898.11.17: 4) is designated here as lectotype. The following MRAC, Tervuren specimens become paralectotypes: 77(117) Manyanga, coll. Wilverth; 166(267) Umangi, coll. Wilverth; 116 Leopoldville, coll. Wilverth and 117 Leopoldville coll. Wilverth.

DIAGNOSIS. The lateral stripes of *Hydrocynus goliath* are the least distinctive within the species of this genus. There are between 2–8 small teeth at the posterior margin of the upper jaw which just protrude through the skin. The anal fin has 3 soft unbranched rays and usually 14 branched rays; in all other *Hydrocynus* species there are usually 12 branched rays.

This species has a higher vertebral count of between 52–54 vertebrae compared with a range of 45–51 vertebrae in other species. Similarly, there are a larger number of scales in the lateral line series, ranging from 53–58 scales, whilst the range for the remaining species is 43–55 scales.



Hydrocyon goliath.

Fig. 27 *Hydrocynus goliath* (taken from Boulenger, 1909 *Catalogue of the freshwater fishes of Africa in the British Museum* p. 185).

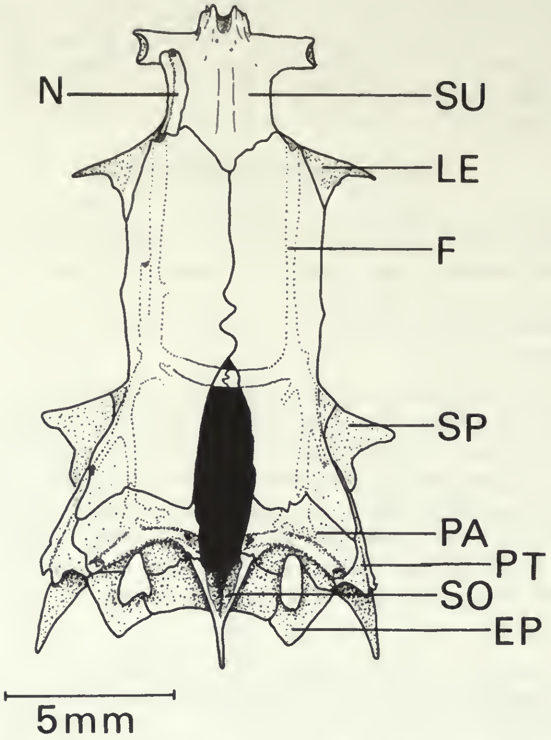


Fig. 28 *Hydrocynus goliath* neurocranium, dorsal view.

Description. Based on the lectotype, paralectotypes and 26 other specimens, ranging in size from 36·1–672 mm standard length. Depth of body 19·4–32·7 (mean = 23) per cent of standard length; length of head 19·2–23·1 (mean = 21·2) per cent. The dorsal profile of the head is straight. Interorbital width 6·2–8·5 (mean = 7·9) per cent; 4th infraorbital width 5·5–8·0 (mean = 6·5); snout length 8·6–10·9 (mean = 9·6) per cent; depth of premaxilla 3·8–4·4 (mean = 4·3) per cent.

Gill rakers: Very short, less than one-third the length of the gill filaments; 8–9 rakers on the first ceratobranchial.
Scales: Lateral line with 53–58 scales, 53 (f. 2), 54 (f. 2), 55 (f. 7), 56 (f. 9), 57 (f. 5), or 58 (f. 4).
Fins: Dorsal fin with 2 soft unbranched rays and 8 branched rays in all specimens examined. Anal with 3 soft unbranched rays and 12 (f. 2), 13 (f. 2), 14 (f. 20), 15 (f. 5) or 16 (f. 1) branched rays.
Teeth: Are like those described for *H. forskahlii* but with 12 (f. 1), 14 (f. 1), 15 (f. 2), 16 (f. 9), 17 (f. 2), 18 (f. 11), 19 (f. 1) or 20 (f. 2) in the upper jaw, and 8 (f. 2), 10 (f. 5), 12 (f. 8), 13 (f. 1) or 14 (f. 13) in the lower jaw.
Vertebrae: 52–54; counted as abdominal + caudal elements: 32 + 20 (f. 1); 33 + 20 (f. 5); 33 + 21 (f. 1); 34 + 19 (f. 1); 34 + 20 (f. 3); 35 + 19 (f. 2) or 36 + 20 (f. 1).
Osteology: The osteology of *H. goliath* differs from the description given for *H. forskahlii* in the following features:
The supraethmoid process has a median groove (Fig. 28) as opposed to the shallow depression characteristic of *H. forskahlii* and *H. brevis*. The frontals are narrow and rectangular unlike the broad rectangular frontals of the other species. There is an edentulous, oval toothplate on basibranchial 4 (Fig. 29) a character which is unique to this species within the characiforms.

Distribution Restricted to the Oubangui R. (Waters, pers. comm.), the central and upper Zaire basin.

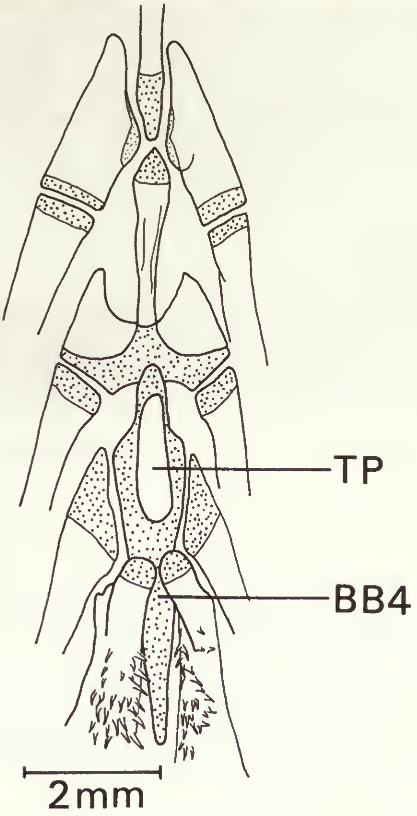


Fig. 29 *Hydrocynus goliath* basibranchial 4, dorsal view.

MATERIAL EXAMINED. BMNH: 1898.11.17: 4 (lectotype) Manyanga Belgian Congo (Zaire); 1919.9.10: 96, Leopoldville (Kinshasa, Zaire); 1907.5.2: 18, Bolobo Belgian Congo (Zaire); 1919.9.10: 97 Busabangi Belgian Congo (Zaire); 1899.8.22: 10, Monsembe Belgian Congo (Zaire); 1901.12.12: 21, Monsembe Belgian Congo (Zaire); 1898.11.17: 5 (syntype of *H. vittiger)*, Manyanga Belgian Congo (Zaire); 1919.9.10: 95, Leopoldville (Kinshasa, Zaire); 1975.6.20: 69, Monganga-Ilewa, Zaire, MRAC: 77 (paralectotype) Manyanga Belgian Congo (Zaire); 166 (paralectotype) Umangi Belgian Congo (Zaire); 74.59.P. 1, Zaire; 189340–341, Kisangani, Zaire; 149 (syntype of *H. vittiger*) Upoto Belgian Congo (Zaire); 165 (syntype of *H. vittiger*) Umangi Belgian Congo (Zaire); 120625 Yangami Belgian Congo (Zaire); 48032 Matadi Belgian Congo (Zaire); 120624 Yangambi Belgian Congo (Zaire); 120622–120623 Yangambi Belgian Congo (Zaire); 48074–48077 R. Kalamu Belgian Congo (Zaire); 2319 Leopoldville (Kinshasa, Zaire). MRHN 10749 Yangambi Belgian Congo (Zaire); 10748, Yangambi Belgian Congo (Zaire); 15238, Leopoldville (Kinshasa, Zaire).

Hydrocynus tanzaniae sp. n. fig. 30

DIAGNOSIS. The lateral stripes of *H. tanzaniae* are distinct and it differs from all other *Hydrocynus* species in the presence of elongated 3rd and 4th dorsal and anal fin rays. It is distinguished from *H. forskahlii* and *H. brevis* by the presence of at least 14 upper and 12 lower jaw teeth and a lateral line scale count of 43–47 scales as compared with 46–55 scales in the other two species. The body is deeper (mean = 23·8 per cent of standard length) than that of *H. forskahlii* (mean = 22·6 per cent of standard length) but does not quite approach the body depth of *H. brevis* (mean = 24·4 per cent of standard length).

Hydrocynus tanzaniae has 3 soft, 12–13 (mode 12) branched anal fin rays compared with 3 soft, 12–16 (mode 14) in *H. goliath.*

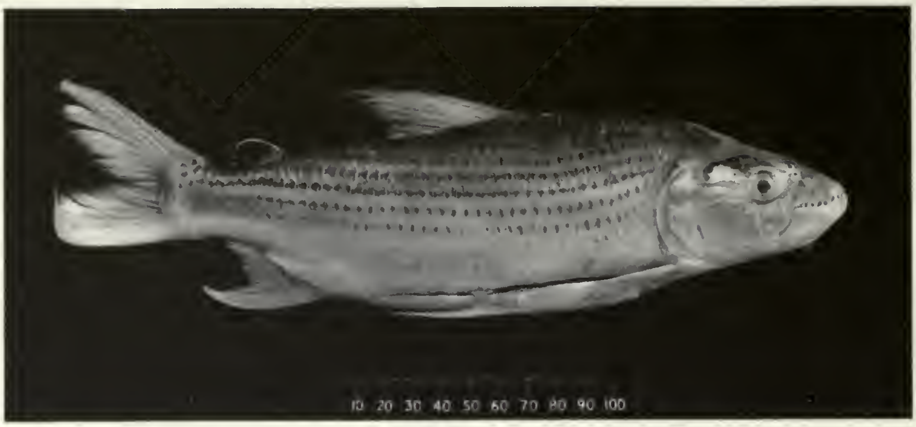

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Fig. 30 *Hydrocynus tanzaniae* n. sp. Holotype BMNH 1976.10.21: 130

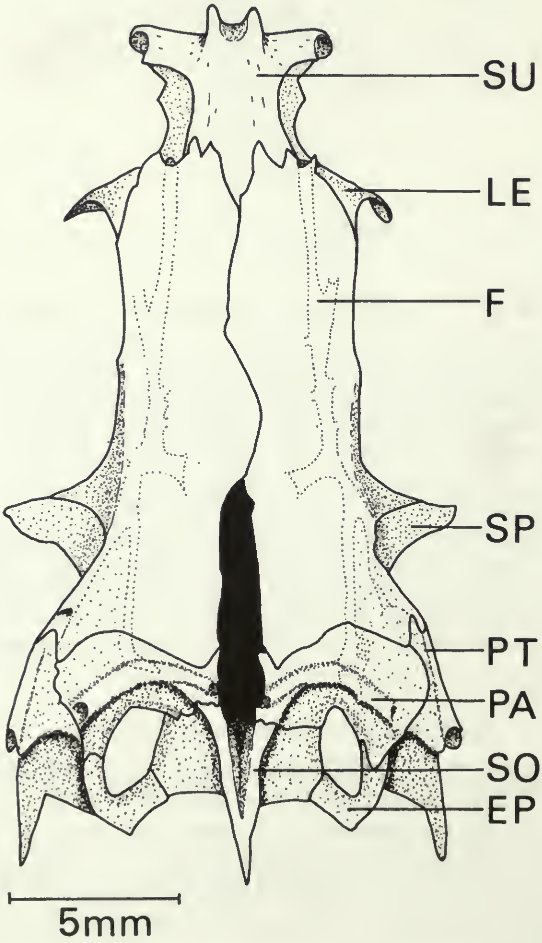
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Fig. 31 *Hydrocynus tanzaniae* neurocranium, dorsal view.

DESCRIPTION. Based on the holotype, a female of 247 mm standard length, from Lower Ruvu River, Tanzania, collected by R. G. Bailey, BMNH 1976.10.21: 130, two paratypes of 141·5 mm and 191 mm standard length from the Rufiji River, Tanzania, collected by A. I. Payne, BMNH 1981.7.7: 41–42, and 17 other specimens.

Depth of body 20·0–26·6 (mean = 23·8) per cent of standard length; length of head 18·3–22·2 (mean = 20·4) per cent. The dorsal profile of the head is straight. Interorbital width 6·5–8·1 (mean = 7·3) per cent; 4th infraorbital width 6·0–7·6 (mean = 6·3) per cent; snout length 7·1–9·0 (mean = 8·0) per cent; depth of premaxilla 2·2–3·4 (mean = 2·7) per cent of standard length.

Gill rakers: Short, approximately one-third the length of the gill filaments; 8–9 (mode 9) rakers on the first ceratobranchial.

Scales: Lateral line with 43–47 scales, 43 (f. 2), 44 (f. 1), 45 (f. 7), 46 (f. 5) or 47 (f. 5).

Fins: Dorsal with 2 soft, unbranched rays and 8 branched rays in all specimens examined. Anal fin with 3 soft, unbranched rays and 12 (f. 16), or 13 (f. 4) branched rays.

Teeth: Similar to those in *H. forskahlii*, with 13 (f. 1), 14 (f. 7), 15 (f. 1) or 16 (f. 11) in the upper jaw and 10 (f. 1) or 12 (f. 19) in the lower jaw.

Vertebrae: 46–47; counted as abdominal + caudal elements: 28 + 18 (f. 1), 28 + 19 (f. 1) or 29 + 17 (f. 2).

Osteology: The osteology of *H. tanzaniae* differs from the description given for *H. forskahlii* in the following features:

The supraethmoid process is deeply notched in the mid-line (Fig. 31) unlike that of *H. forskahlii* and *H. brevis* which has a shallow depression or *H. goliath* which has a median groove. The lateral supraethmoid wings are anterolaterally orientated (Fig. 31) and the supraethmoid is narrow posteriorly so that in dorsal view part of the dorsal surface of the vomer is visible. The lateral supraethmoid wings of the other *Hydrocynus* species are horizontal, the supraethmoid obscures the vomer in dorsal view and is not markedly narrow.

DISTRIBUTION. The eastward flowing rivers of Tanzania, in the Wami Ruaha and Rufiji river systems.

MATERIAL EXAMINED. BMNH: 1976.10.21: 130 (holotype), Lower Ruvu river; 1981.7.7: 41–42 (paratypes), Rufiji River; 1976.10.21: 128–129, Lower Ruvu R.; 1972.11.28:3–4, Ruaha R.: 1981.1.14: 44 Kilombero R.; 1981.1.14. 45–46, Kilombero R.; 1981.1.14: 33–43 Makulinzo. MRAC 188963–968, Gt Ruaha R.; 191468, Ruaha R.

Nomen dubium

Salmo dentex (non Linnaeus) Forsskål, 1775 *Descriptiones Animalium* p. 67, number 97.

The type of *Salmo dentex* is no longer extant (Klausewitz & Nielsen, 1965); however, Forsskål's description of this Nilotic fish clearly refers to a specimen of *Hydrocynus*. *Salmo dentex* is usually included in the synonymy of *H. forskahlii* but I consider it a *nomen dubium* since both *H. forskahlii* and *H. brevis* are sympatric in the Nile and there are insufficient data in Forsskål's description to assign his material to one or other of the two species.

Key to species

The description of the four species of *Hydrocynus* recognized here are summarized as follows:

1 Usually with 14 or more teeth in the upper jaw 2
– Usually with 12 teeth in the upper jaw 3
2 Gill rakers very short, less than one-third the length of the gill filaments; lateral line with 53–58 pored scales; anal fin with 3 soft, unbranched and usually 14 branched rays; vertebrae 52–54; lateral stripes not distinctive; found in the Oubangui R., central and upper Zaire . . . . . ***H. goliath***

– Gill rakers approximately one-third the length of the gill filaments; lateral line with 43–47 pored scales; anal fin with 3 soft, unbranched and usually 12 branched rays; vertebrae 46–47; lateral stripes distinct; confined to the eastward flowing rivers of Tanzania . . . . ***H. tanzaniae***

3 Gill rakers long, approximately equal in length to the gill filaments; 4th infraorbital width approximately 6·1 per cent (range 5·1–7·5 per cent) of the standard length; body not deep, usually 22·6 per cent of the standard length (range 17·2–27·8 per cent of SL); lateral line with 46–53 pored scales; vertebrae 45–51; lateral stripes prominent; widespread throughout Africa . . . . ***H. forskahlii***

– Gill rakers approximately one-third the length of the gill filaments; 4th infraorbital broad, approximately 7·7 per cent of standard length (range 6·9–8·9 per cent of SL); body deep, approximately 24·4 per cent of standard length (range 19·1–29·6 per cent of SL); lateral line with 47–55 pored scales; vertebrae 49–51; lateral stripes conspicuous; found from the Nilo-Sudan region to the west coast of northern Africa . . . . ***H. brevis***

Concluding remarks

An osteological study of four *Hydrocynus* species has revealed eighteen features which appear to be autapomorphic for the genus.

In view of Roberts's (1966, 1967 & 1969) idea of relationship between *Alestes* and *Hydrocynus*, species of the former taxon were examined in detail. During the course of this study it became apparent that Roberts's *Alestes* (*sensu* Boulenger, 1907) is a non-monophyletic assemblage, containing species having their affinities with species in at least three other genera. Of those genera, *Alestes sensu stricto* (see p. 190) is, on the basis of three synapomorphies, apparently the sister-group of *Hydrocynus* (see p. 192). However, the relationship of *Hydrocynus* and *Alestes s.s.* to the *Alestes sensu lato* group of species cannot be resolved until a detailed anatomical revision and phylogenetic analysis of all their constituent species has been undertaken.

Roberts (1969: 441) commented on the upper jaw morphology of African Characidae, and pointed out that the morphology of the premaxilla and maxilla differs from that of the Neotropical Characidae. Amongst outgroup Neotropical characids examined, I find the maxilla is typically dentate, large, ovate and lamellar, with a medially directed ascending process. The maxilla of the African Characidae (excluding *Hydrocynus*, see p. 172) is edentulous, pediculate posteriorly, and has a well-developed, anteriorly curved ascending process; possibly this represents the derived condition within the Characiformes.

The majority of Characiformes have two posttemporal fossae, although in concurrence with Vari (1979: 341) I find that with the exception of *Lepidarchus*, all African Characidae have a third posttemporal fossa contained entirely within the epioccipital. A third posttemporal fossa contained entirely within the epioccipital occurs in the Neotropical characiform families Hemiodontidae, Paradontidae and Curimatidae (Roberts, 1974: 416 & 425; Vari, 1983: 37).

The African characiform families Distichodontidae and Citharinidae and the neotropical characid tribe Cynodontini, also have a third posttemporal fossa, but it is bordered by both the epioccipital and exoccipital bones (Vari, 1979: 289; 1983: 37).

Vari (1983) gives a series of characters uniting the Curimatidae to the Prochilodontidae; the Hemiodontidae have a rhinosphenoid bone present, in common with various other Neotropical characids. In the absence of any synapomorphies indicating a close relationship between the Hemiodontidae, Parodontidae, Curimatidae and the African Characidae, the presence of a third posttemporal fossa contained entirely within the epioccipital is most parsimoniously explained as a homoplasy.

Sexual dimorphism in the posterior neural spines (see p. 183), occurs in all African Characidae examined (with the notable exception of *Lepidarchus*) and in one genus (*Curimatopsis*) of the Neotropical characiform family Curimatidae (Vari, 1982, 4). The morphology of these modified neural spines in *Curimatopsis*, however, differs from that in the African Characidae (see p. 192). Thus, it is unlikely this feature represents a synapomorphy uniting the African Characidae with the Curimatidae. The particular morphology of the modified neural spines, shared only amongst African characids, indicates that this character is synapomorphic for those taxa possessing it, namely *Hydrocynus, Alestes sensu stricto, Alestes sensu lato, Bryconaethiops, Micralestes* and *Rhabdalestes*.

The African characid genus *Lepidarchus* apparently lacks all those features hypothesized above as synapomorphies for African Characidae. It is, therefore possible either that *Lepidarchus* should not be included in the family Characidae, or since it shows reduction in many morphological features, this genus is paedomorphic and represents a miniaturized characid.

The unique upper jaw morphology, absence of ectopterygoid teeth (see p. 189) and secondary sexual dimorphism exhibited in the posterior neural spines are hypothesized to be synapomorphies that indicate the African characids form a monophyletic subunit within the Characiformes, an idea already suggested by Vari (1979: 342). However, since a number of African characid genera were unavailable for outgroup comparison, formal designation of such a category cannot be made at this stage.

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References

Agassiz, L. 1829. *In* J. B. De Spix, *Selecta genera et species piscium, quos in itinere per Brasilium*. Monachii.

Barnard, K. H. 1948. Report on a collection of fishes from the Okovango River, with notes on Zambesi· fishes. *Annals of the South African Museum* **36** (5): 407–458.

Begg, G. W. 1973. Some abnormalities and an interesting anatomical feature occurring in the tigerfish *Hydrocynus vittatus* at Lake Kariba. *Piscator* no. 86: 110–112.

Bertin, L. 1939. Catalogue des types de poissons du Museum National d'Histoire Naturelle. 3e partie Ostariophysaires (Characiniformes Gymnotiformes). *Bulletin du Museum d'Histoire Naturelle,* Paris 2e serie 11: 1–49.

Boulenger, G. A. 1901. *Les poissons du Congo*. Brussels 1–532.

—— 1907. *Zoology of Egypt: The fishes of the Nile*. Published by the Egyptian Government.

—— 1909. *Catalogue of the freshwater fishes of Africa in the British Museum*. London.

Cuvier, G. 1817. *Le regne animal distribue d'apres son organisation pour servir de base a l'histoire naturelle des animaux et d'introduction a l'anatomie compares*. Deterville, Paris. pp. 167–168.

—— 1819. Sur les poissons du sous-genre *Hydrocyon,* sur deux nouvelles especes de *Chalceus,* sur trois nouvelles especes de Serrasalmes, et sur l'*Argentine glossodonta* de Forskahl, qui est l'*Albula gonorhynchus* de Bloch. *Memoires du Muséum d'Histoire Naturelle, Paris*. **5**: 351–379.

Daget, J., Gosse, J. P. & Thys van den Audenaerde, D. F. E. (Eds). 1984. Check-list of the freshwater fishes of Africa. **1**: 1–410 ORSTOM Paris MRAC Tervuren.

Dingerkus, G. & Uhler, L. D. 1977. Enzyme clearing of alcian blue stained whole small vertebrates for demonstration of cartilage. *Stain Technology* **52** (4): 229–232.

Eastman, C. R. 1917. Dentition of *Hydrocyon* and its supposed fossil allies. *Bulletin of the American Museum of Natural History* **37**: 757–760.

Fink, W. L. 1981. Ontogeny and phylogeny of tooth attachment modes in Actinopterygian fishes. *Journal of Morphology* **167**: 167–184.

Fink, S. V. & Fink, W. L. 1981. Interrelationships of the ostariophysan fishes (Teleostei). *Zoological Journal of the Linnean Society* **72**: 297–353.

Forsskål, P. 1775. *Descriptiones animalium avium, amphibiorum, piscium insectorum, vermium; quae in itinere or entali observavit. Post mortem auctoris edidit Carsten Neibuhr*. Havniae. p. 66 number 97.

Geoffroy St-Hilaire, E. 1809. Poissons du Nil. In *Description de l'Egypte . . . Histoire Naturelle*. **24**: 236–244. Paris 1809.

Géry, J. 1968. Un essai de systematique quantitative: La classification des especes du genre *Alestes s. lat.* (Pisces, Characoidei). *Vie et Milieu, Serie A: Biologie marine* **19**: 171–194.

—— 1977. *Characoids of the world.* T. F. H. Publications, Inc. Ltd. (Gt Britain).

Greenwood, P. H., Rosen, D. E., Weitzman, S. H. & Myers, G. S. 1966. Phyletic studies of teleostean fishes, with a provisional classification of living forms. *Bulletin of the American Museum of Natural History* **131**: 339–456.

Günther, A. 1864 *Catalogue of fishes* **5**: 277–380.

Hasselquist, F. 1757. *Iter Palestinum* . . . Stockholm.

Howes, G. J. 1978. The anatomy and relationships of the cyprinid fish *Luciobrama macrocephalus* (Lacepede). *Bulletin of the British Museum (Natural History)* Zoology **34** (1): 1–64.

—— 1981. Anatomy and phylogeny of the Chinese major carps *Ctenopharyngodon* Steind., 1866 and *Hypophthalmichthys* Blkr., 1860. *Bulletin of the British Museum (Natural History)* Zoology **1** (1): 1–52.

Johnels, A. G. 1954. Notes on fishes from the Gambia river. *Arkiv for Zoologi* **6**: 131–164.

Kampf, W. D. 1961. Vergleichende funktionsmorphologische Untersuchungen an den Viscerocranien einiger rauberisch lebender Knochenfische. *Zoologische Beitrage N. F.* **6**: 391–496.

Klausewitz, W. & Nielsen, J. G. 1965. On Forsskals collection of fishes in the Zoological Museum of Copenhagen. *Spolia Zoologia Musei Hannienensis* **22**: 5–29.

Lacepède, B. G. E. de la Ville-sur-Illon. 1803. *Histoire naturelle des Poissons*, **V**: p. 269.

Myers, G. S. 1929. Cranial differences in the African characin fishes of the genera *Alestes* and *Brycinus* with notes on the arrangement of related genera. *American Museum Novitates* **342**: 1–7.

—— 1950. On the characid fishes called *Hydrocynus* and *Hydrocyon* by Cuvier. *Proceedings of the California Zoological Club*. **1** (9): 45–47.

—— 1958. Trends in the evolution of teleostean fishes. *Stanford Ichthyological Bulletin* **7** (3): 27–30.

—— & Weitzman, S. H. 1960. A Brazilian pike-characid, *Boulengerella lateristriga* rediscovered in the Rio Negro. *Stanford Ichthyological Bulletin* **7**: 201–205.

Nelson, G. J. 1973. Relationships of clupeomorphs with remarks on the structure of the lower jaw in fishes. *Zoological Journal of Linnean Society* **53** (Supplement 1): 333–349.

Patterson, C. 1975. The braincase of pholidophorid and leptolepid fishes with a review of the actinopterygian braincase. *Philosophical Transactions of the Royal Society* **B 269** (899): 275–579.

Poll, M. 1976. *Exploration du Parc National de l'Upemba. Mission de G. F. de Witte*. fasc. 73: 1–127.

Roberts, T. R. 1966. Description and osteology of *Lepidarchus adonis* a remarkable new characid fish from West Africa. *Stanford Ichthyological Bulletin* **8**: 209–227.

—— 1967. Tooth formation and replacement in characoid fishes. *Stanford Ichthyological Bulletin* **8**: 231–247.

—— 1969. Osteology and relationships of characoid fishes particularly the genera *Hepsetus, Salminus, Hoplias, Ctenolucius* and *Acestrorhynchus*. *Proceedings of the California Academy of Sciences*. 4th series **36** (15): 391–500.

—— 1974. Osteology and classification of the neotropical characoid fishes of the families Hemiodontidae (including Anodontinae) and Parodontidae. *Bulletin of the Museum of Comparative Zoology* **146** (9): 411–472.

Rüppell, E. 1829. *Beschreibung und Abildung mehrerer neuer Fische, im Nil entdeckt*. 1–28.

Starks, C. E. 1926. Bones of the ethmoid region of the fish skull. *Stanford University Publications. Biological Sciences* **4** (3): 143–338.

Svensson, G. S. O. 1933. Freshwater fishes from the Gambia river. *Kungliga Svenska Vetenskapsakademiens Handlingar*. **12**: 1–102.

Travassos, H. 1962. Catalogo dos generos e subgeneros da subordem Characoidei. *Dusenia* **3** (2): 77–116.

Tweddle, D. 1982. Tooth replacement in the tigerfish *Hydrocynus vittatus* Castelnau. *Journal of Science and Technology (Malawi)* **3** (1): 33–35.

Valenciennes, A. 1849. In: Cuvier and Valenciennes: *Histoire Naturelle des Poissons, Paris*. **22**: 307–316.

Vari, R. P. 1979. Anatomy, relationships and classification of the families Citharinidae and Distichodontidae (Pisces, Characoidea). *Bulletin of the British Museum (Natural History)*. Zoology **35** (5): 261–344.

—— 1982. Systematics of the neotropical characoid genus *Curimatopsis* (Pisces: Characoidei). *Smithsonian Contributions to Zoology* no. **373**: 1–28.

—— 1983. Phylogenetic relationships of the families Curimatidae, Prochilodontidae, Anostomidae and Chilodontidae (Pisces: Characiformes). *Smithsonian Contributions to Zoology* no. **378**: 1–60.

Weitzman, S. H. 1962. The osteology of *Brycon meeki*, a generalized characid fish, with an osteological definition of the family. *Stanford Ichthyological Bulletin* **8** (1): 1–77.

—— **& Fink, W. L.** 1983. Relationships of the neon tetras, a group of South American freshwater fishes (Teleostei, Characidae) with comments on the phylogeny of New World characiforms. *Bulletin of the Museum of Comparative Zoology* **150** (6): 339–395.

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Appendix 1

MATERIAL EXAMINED

EtOH = ethanol preserved; A = Alcian blue/Alizarin red stained; S = skeleton

Characidae			
Alestes affinis		A	
Alestes ansorgii		A	
Alestes baremose	EtOH	A	S
Alestes chaperi		A	
Alestes dentex	EtOH	A	S
Alestes ferox		A	
Alestes humilis		A	
Alestes imberi		A	
Alestes jacksoni		A	
Alestes lateralis		A	
Alestes leuciscus		A	
Alestes liebrechtsii	EtOH	A	
Alestes macrolepidotus		A	S
Alestes macrophthalmus	EtOH	A	S
Alestes minutus	EtOH	A	
Alestes stuhlmanni	EtOH	A	
Brycondethiops microstoma	EtOH	A	S
Micralestes acutidens		A	S
Rhabdalestes rhodesianus	EtOH	A	
Hemigrammopetersius barnardi	EtOH	A	
Phenacogrammus interruptus		A	
Virilia pabrensis	EtOH	A	
Alestopetersius leopoldianus			S
Lepidarchus adonis	EtOH	A	
Serrasalmus humeralis	EtOH		S
Rhaphiodon vulpinus			S
Hydrolycus scomberoides			S
Hydrolycus pectoralis			S
Charax gibbosus			S
Acestrorhynchus falcatus			S

continued overleaf

Appendix 1—*continued*

EtOH = ethanol preserved; A = Alcian blue/Alizarin red stained; S = skeleton

Oligosarcus bolivianus		A	S
Oligosarcus hepsetus			S
Roeboides sp			S
Salminus maxillosus			S
Brycon falcatus		A	S
Brycon dentex			S
Triportheus angulatus			S
Poptella orbicularis			S
Astyanax bimaculatus		A	S
Moenkhausia lepidura			S
Bryconops caudomaculatus			S
Scissor macrocephalus			S
Hepsetidae			
Hepsetus odoe	EtOH	A	S
Distichodontidae			
Distichodus lusosso			S
Xenocharax spilurus			S
Ichthyborus besse			S
Ichthyborus quadrilineatus			S
Citharinidae			
Citharinus citharus			S
Erythrinidae			
Erythrinus erythrinus		A	
Hoplias malabaricus		A	S
Hoplerythrinus unitaeniatus		A	S
Ctenoluciidae			
Ctenolucius sp			S
Boulengerella lucium			S
Lebiasinidae			
Lebiasina multimaculata			S
Lebiasina erythrinoides			S
Curimatidae			
Curimatorbis spilurus			S

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Dr Ethelwynn Trewavas

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Three genera of the mouth-brooding species are included though in one of them, *Danakilia*, the single species is too small to warrant farming. The other two, *Sarotherodon*, with nine species and *Oreochromis*, with thirty-one, are distinguished primarily by their breeding habits and their biogeography, supported by structural features. Each species is described, with its diagnostic features emphasised and illustrated, and to this is added a summary of known ecology and behaviour. Conclusions on relationships involve assessment of parallel and convergent evolution. Dr Trewavas writes with the interests of the fish culturists, as well as those of the taxonomists, very much in mind.

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A taxonomic revision of the southern Arabian Enidae *sensu lato* (Mollusca; Pulmonata)

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Introduction

Although characterised by relatively low levels of faunal diversity, the Arabian peninsula occupies an important geographic position at the boundary of three of the world's major biogeographic zones—the Palaearctic, Afrotropical, and Oriental. It is a region of taxonomic and biogeographic discontinuity, not only for land molluscs (Mordan, 1980*b*) but also for many other taxa. Whilst land snails show remarkable distributional stability through time (Solem, 1979), and thus represent a highly suitable group for biogeographic analysis, the value of their contribution to many such studies has been limited by the inadequacy of our knowledge of their taxonomy (Peake, 1978).

The non-marine Mollusca of southern Arabia, an area defined here broadly as that part of the peninsula south to the Tropic of Cancer but including the whole of Oman, were last comprehensively reviewed by Connolly (1941). To the end of this paper Connolly appended a list of 164 species of land and freshwater Mollusca from the region, with the pertinent comment that, of those species whose distribution is restricted to southern Arabia, 'half the names are probably superfluous and should be relegated to synonymy' (Connolly, 1941:40). Although a small number of junior synonyms were included, the list remained essentially uncritical. Subsequently a

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series of regional reviews has appeared covering South Yemen and Dhofar (Fischer-Piette & Métivier, 1972), North Yemen (Verdcourt, 1974), Saudi Arabia (Mordan, 1980*a*), and Oman (Smythe & Gallagher, 1977; Mordan, 1980*b*), but all are based essentially on conchological material.

Members of the family Enidae *s.l.* consitute by far the most numerous single element in the southern Arabian land-snail fauna, accounting for well over one-third of the total number of terrestrial species listed by Connolly. In an earlier paper (Mordan, 1984) the status of subfamily units within the Enidae was considered, with especial reference to the Arabian fauna, and the anatomical differences between the groups summarised. On the basis of these differences, particularly of the reproductive and pallial systems, two major groupings were recognised: the northern Enidae *s.s.* comprising the subfamilies Chondrulinae and Eninae, as defined by Forcart (1940); and the southern Cerastinae *sensu* Zilch (1959). These two groups have broadly non-overlapping ranges, but both are represented in southern Arabia. From the analysis it was also concluded that there was no evidence for the two being sister groups in a cladistic sense, and thus the Enidae *s.l.* could not be considered a monophyletic taxon. Formalising the status of the Cerastinae has, however, been deferred until there is a greater knowledge of the related orthurethran families, and consequently the present paper retains all three subfamilies within the Enidae *s.l.*. The biogeographic implications of these conclusions were considered in some detail in the earlier paper and will not be repeated here. The name Cerastinae Wenz, 1923 is used as it has priority over Pachnodinae Steenberg, 1925, and has the type genus *Cerastus* Albers, 1860; *Cerastus* Dejean, 1821 must be considered a *nomen nudum* under Article 12 of the International Code of Zoological Nomenclature.

The present paper is a review of the taxonomy of the Arabian enids using the admittedly incomplete anatomical information available. Whilst it is primarily concerned with genus- and species-level distinction, the opportunity is taken to discuss, in greater detail than was possible in the earlier paper, the anatomical characters relevant to the higher-level taxonomy of the Enidae as exemplified by the Arabian forms. No analysis of phylogeny has been attempted as this will form the subject of a further paper reviewing all cerastine genera.

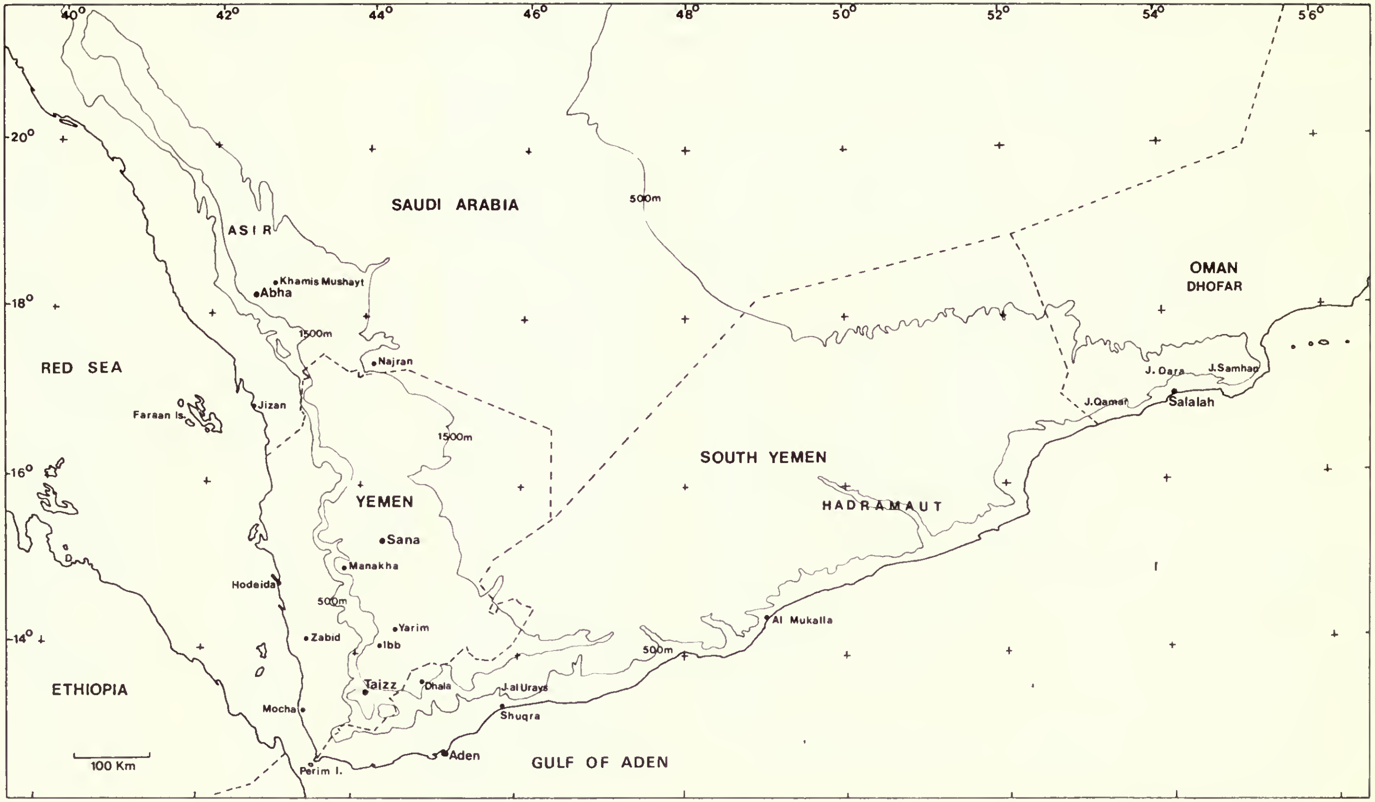
The work is based primarily on three collections in the British Museum (Natural History) [BMNH]: the collection made by Hugh Scott in North and South Yemen, recently supplemented by spirit material collected by Peter Heath in the environs of Taizz, N. Yemen in 1978–9; material obtained by the author from Dhofar in 1976; and a comprehensive collection made throughout Oman by Major Michael Gallagher from 1976 onwards.

Additional material, including many important types, has been loaned from the following institutions: Muséum National d'histoire Naturelle, Paris [MNHN]; Royal Scottish Museum, Edinburgh [RSM]; Zoological Museum, Copenhagen [ZMC]; Muséum d'histoire Naturelle, Geneva [MHNG]; Academy of Natural Sciences, Philadelphia [ANS]; National Museum of Wales, Cardiff [NMW]; and Zoologisches Museum, Berlin [ZMB].

All conchological measurements are expressed in millimetres as follows: shell height × max. shell width × min. shell width; aperture height × aperture width; lip width (if developed); number of whorls.

e.g. 23·1 × 10·2 × 9·4; 9·5 × 7·0; lip 1·2; 6·7 wh.

Considerable problems have been encountered with Arabic place names and several localities could not be traced. In particular it has not proved possible to determine the precise location of 'Senna', the type locality of *Cerastus dinshawi* Sykes, 1903; nor a number of Waterson's localities in Saudi Arabia and Yemen. In the lists of material, locality names have been copied directly from the original labels in almost all cases, but in discussing distributions in the text, spelling have usually been taken from the comprehensive edition of the *Times Atlas of the World*, 1968. In particular, the Yemen Arab Republic is referred to as Yemen and the Peoples Republic of South Yemen (formerly the Western Aden Protectorate) as South Yemen. Muscat and Oman is simply called Oman. Maps of south-western Arabia and of northern Oman showing the principal locations are given in Figs 1 and 2.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OMAN
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RED SEA
Najran
J. Qara
J. Samhan
Jizan
Faraan Is.
J. Qamar
Salalah
1500m
SOUTH YEMEN
YEMEN
HADRAMAUT
Sana
Manakha
Hodeida
500m
Yarim
Zabid
Ibb
Al Mukalla
500m
ETHIOPIA
Taizz
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Mocha
Shuqra
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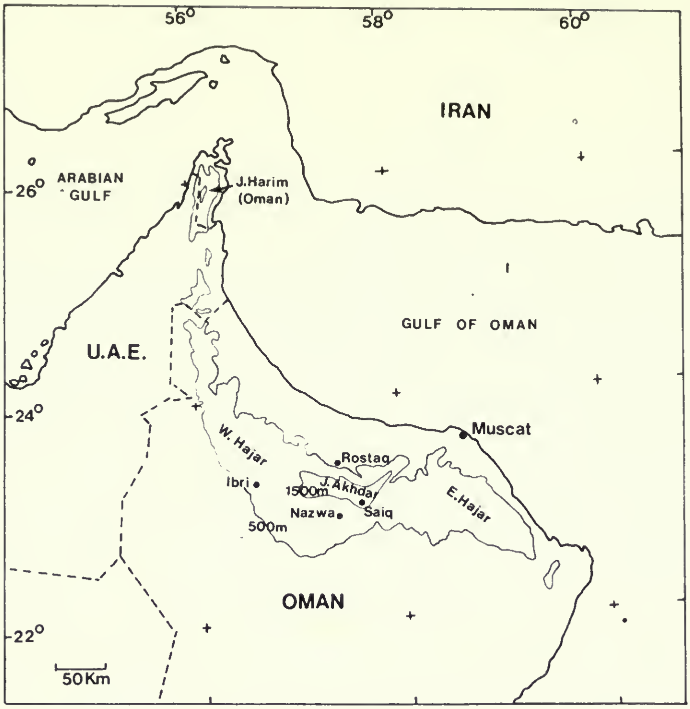
Aden
Perim I.
GULF OF ADEN

Fig. 1 Map of south-west Arabia showing principal locations.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60°
IRAN
ARABIAN GULF
26°
J.Harim (Oman)
GULF OF OMAN
U.A.E.
24°
Muscat
W.Hajar
Rostaq
J.Akhdar
Ibri
1500m
Nazwa
Saiq
500m
E.Hajar
OMAN
22°
50Km

Fig. 2 Map of northern Oman showing principal locations.

Systematic account

Family **ENIDAE** *sensu lato*

Subfamily **CHONDRULINAE** Wenz, 1923

Diagnosis. Kidney orthurethrous, lung with short renal groove but lacking rectal fold. Hermaphrodite duct with clump of culs-de-sac above seminal vesicle; spermoviduct with serous canal; penis without appendix.

MASTUS Beck, 1837

Type species. *Helix pupa* Brugière [subs. desig. Herrmannsen, 1847].

Diagnosis. Penis without appendix, but with large, pointed papilla. Spermatheca with diverticulum.

Mastus omanensis (Smith, 1894)

Buliminus omanensis Smith, 1894:141, fig. 1. [Green Mountain, Oman].
Buliminus omanensis Smith. Smythe & Gallagher, 1977:223, pl. 1.

Type material. Lectotype (here designated, BMNH 1894.3.22.5) and 4 Paralectotypes (BMNH 1894.3.22.6–9), Green Mountain, (Jebel Akhdar, Oman), leg. Jayakar.

Other material. **Oman:** Nazwa, leg. Jayakar, BMNH 1900.6.8.39–41, (3 specs.); Yika, 400 m., leg. M. D. Gallagher, 19.xi.1976, BMNH, (16 specs, 4 dissected); Ghafdi, Wadi Bani Ghafir, 400 m., leg. M. D. Gallagher, BMNH, (24 specs, 2 dissected); Gabet Al Habina, 2100 m., leg. M. D. Gallagher, 29.xi.1977,

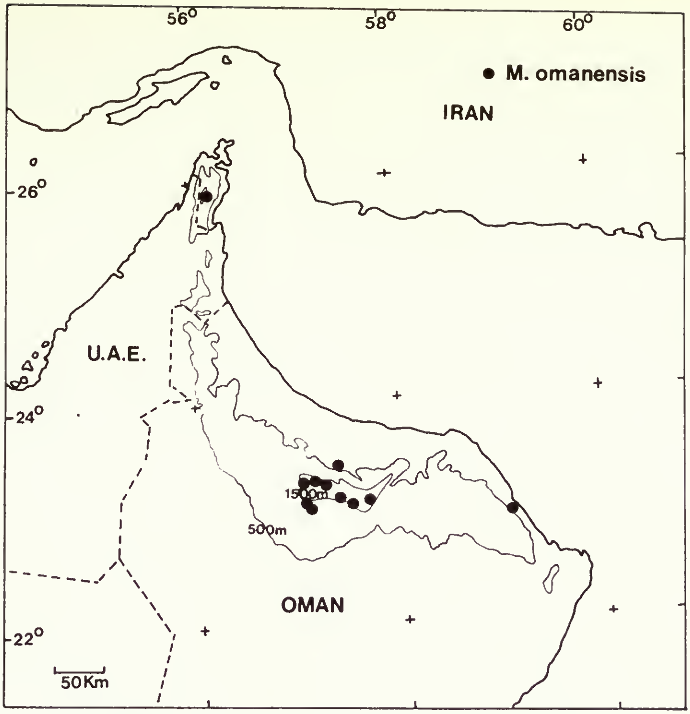


Fig. 3 Distribution map of *Mastus omanensis.*

BMNH, (23 specs.); Jabal Sirah, 2200 m., leg. M. D. Gallagher, 12.vii.1977, BMNH, (1 spec.); 15.v.1978, BMNH, (6 specs.); Jabal Harim, Ruus al Jibaal, 1800–2000 m., leg. M. D. Gallagher & J. P. Manderville, 27.ii.1979, BMNH, (8 specs, 1 spirit); Quasaydot, Ruus al Jibaal, 950 m., leg. M. D. Gallagher, 5.iii.1979, BMNH, (1 shell fragment); Jabal Akhdar, 1400 m, leg. M. D. Gallagher, 8.vi.1979, BMNH, (1 spec.); Jabal Kawr, 2800 m, leg. R. P. Whitcomb, 22.x.1979, BMNH (1 spec.); Wadi Saiq, 1800 m, leg. M. D. Gallagher, 21.iii.1981, BMNH (15 specs.); Wadi Harabin, E. Hajar Mts., 110 m, leg. M. D. Gallagher, 28.viii.1981, (3 specs.); Wakan, leg. M. D. Gallagher, 26.iii.1982, BMNH, (6 specs, 1 dissected).

DISTRIBUTION (Fig. 3). With the exception of synanthropic lowland sites (between 110–400 m above sea level) such as Yika, Ghafdi and Wadi Harabin (all cultivated habitats), the species appears to be restricted to areas above 1500 m in the Jebel Akhdar and Jebel Harim ranges of northern Oman.

DESCRIPTION. Dextral, cylindrical conic *with blunt, rounded apex*; surface glossy with irregular transverse striae and numerous fine, denser spiral striae; protoconch smooth; umbilicus closed. Aperture oval with reflexed lip; callus often extending across parietal wall. Colour uniform pale brown to opaque white, protoconch darker brown.

Shell. Dimensions of Lectotype (Fig. 4a): 23·9 × 12·2 × 9·7; 12·1 × 9·8; lip 2·2; 6·9 wh. Paralectotypes: 21·2 × 11·2 × 9·5; 10·8 × 7·7; lip 2·0; 6·5 wh.; 21·6 × 11·9 × 9·0; 10·8 × 8·1; lip 1·6; 6·6 wh.; 21·9 × 1·9 × 9·3; 10·8 × 8·9; lip 1·9; 6·6 wh.; 20·2 × 11·4 × 9·0; 11·0 × 8·5; lip 1·9; 6·1 wh.

Although there was generally rather little variation in shell size, and more particularly shape (Table 1), a sample of three shells from Wadi Harabin in the eastern Hajar mountains were quite exceptionally small, the dimensions of the smallest adult shell being: 12·3 × 7·3 × 6·9; 6·9 × 5·6; lip 1·2, wh. 5·3. This may be accounted for by the extremely low elevation of the site, 110 m, where moisture levels are almost certainly considerably lower than at the more usual elevations for this species of between 1500–3000 m, even though the locality was a terraced cultivation.

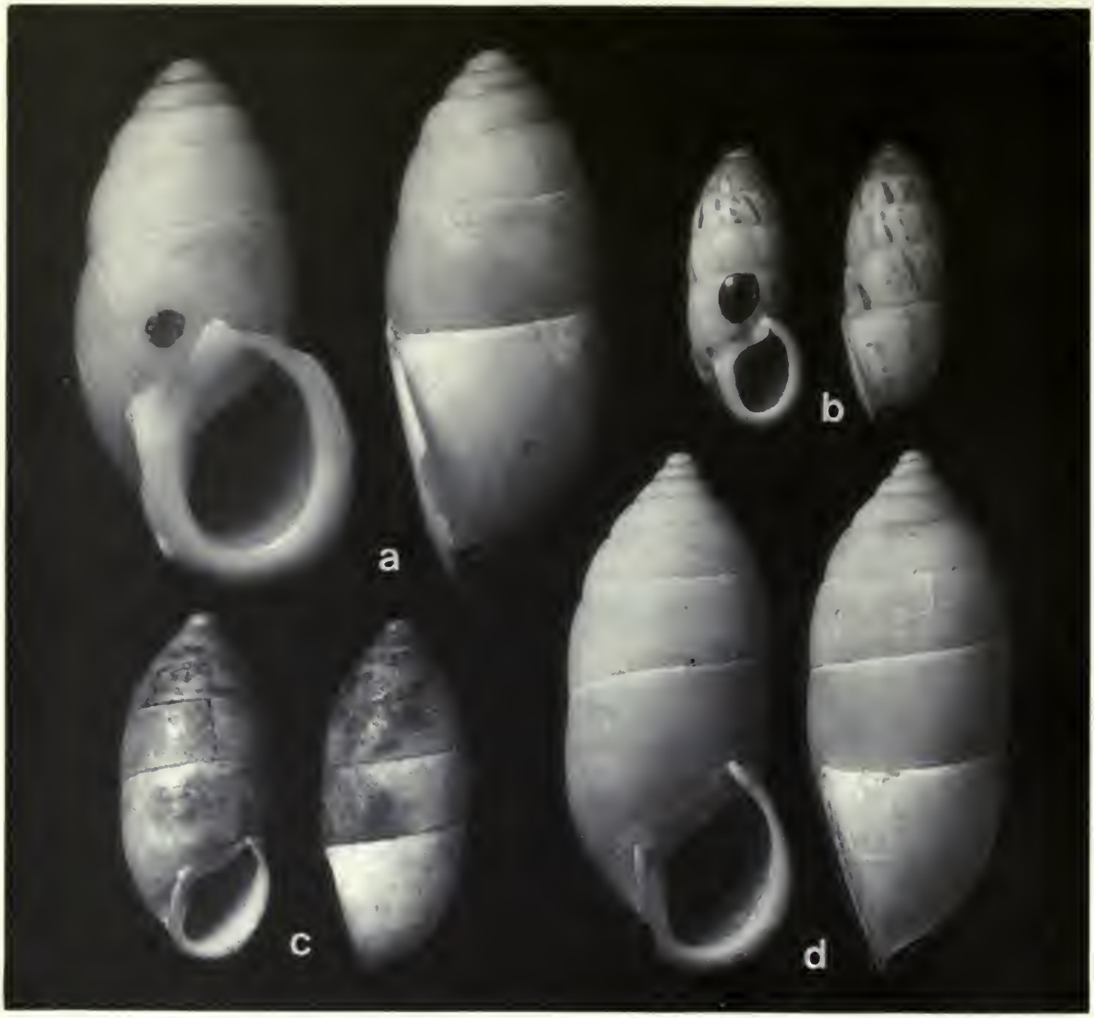


Fig. 4 a, Lectotype of *Buliminus omanensis* Smith, BMNH 1894.3.22.5; b, lectotype of *Buliminus jousseaumei*, BMNH 1894.3.22.10; c, holotype of *Buliminus hedjazicus* Bourguignat, MHNG; d, lectotype of *Bulimus sabaeanus* Bourguignat, MHNG. All × 3.

Table 1 Comparison of shell dimensions of living *Mastus omanensis* from sites in Jebel Akhdar, northern Oman, using Analysis of Variance.

Parameter	Yika, 19.xi.1976 (n = 7)		Wakan, 26.iii.1982 (n = 6)		Ghafdi, 29.xi.1977 (n = 6)		F (d.f. 2, 16)
	x	sd	x	sd	x	sd	
Shell ht..	17·83	1·26	19·62	0·92	18·0	0·93	4·53 *
Shell diam.	10·70	0·3	10·76	0·6	10·28	0·34	2·78 ns
Apert. ht.	9·3	0·61	9·95	0·95	9·55	0·51	1·14 ns
Apert. diam.	7·67	0·6	7·85	0·56	7·75	0·45	0·14 ns
Spire Index	1·75	0·11	1·83	0·11	1·75	0·07	1·35 ns

* = $p < 0{\cdot}05$
ns = not significant.

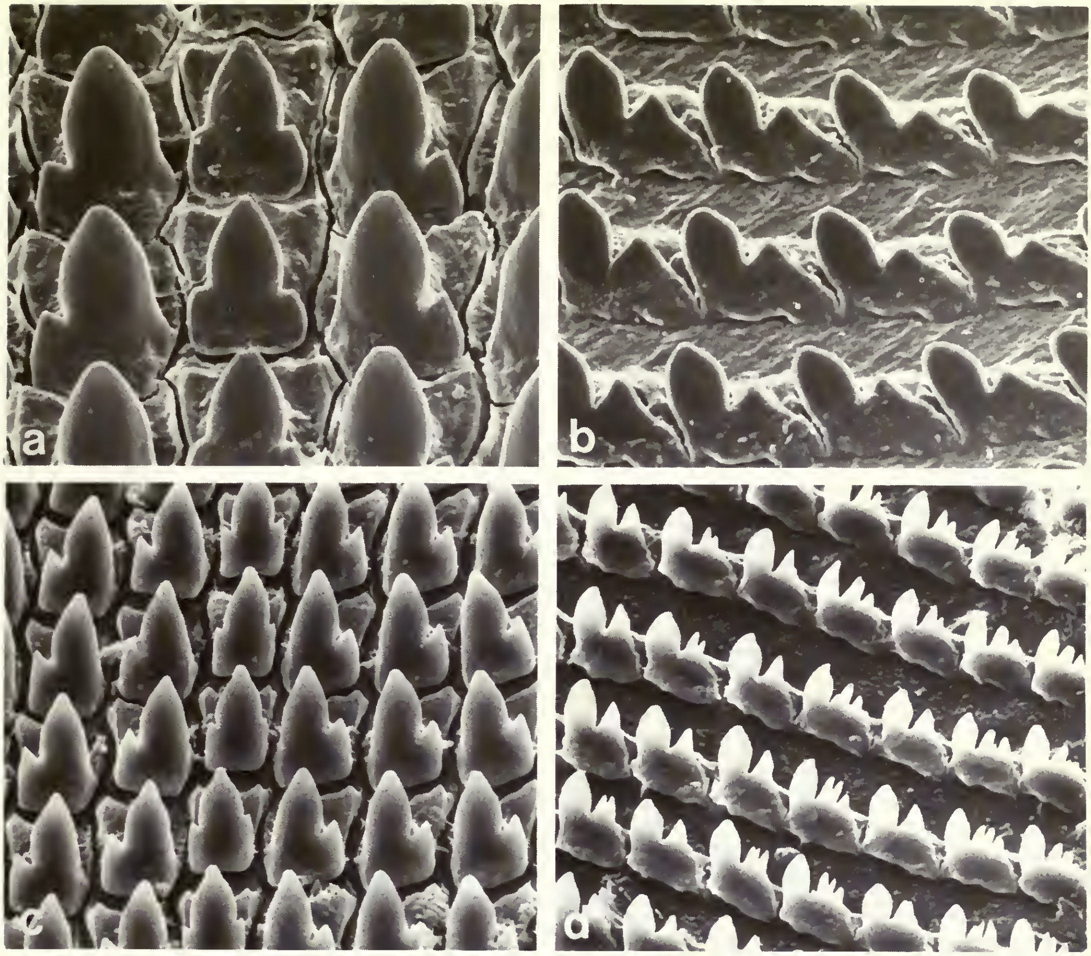


Fig. 5 Radular teeth of northern Oman Enidae: a, *Mastus omanensis,* Yika, 19.xi. 1976, central and lateral; b, marginal; c, *Imparietula jousseaumei,* Rostaq, central and lateral; d, marginal; × 720.

Body. Uniformly cream in colouration.

Radula. (Figs. 5a–b; Table 2). Central tooth noticeably smaller than laterals, and ectocones of central relatively reduced. Marginal teeth with very blunt mesocone and wide, pointed ectocone which only becomes bicuspid in last three or four teeth in row. Basal plates quadrate and extremely broad.

Lung cavity (Fig. 6A). Similar in morphology to *Imparietula jousseaumei,* but occupying only a little over one whorl (Table 3); relatively longer kidney extending 0·95 times cavity length. A shallow groove runs from renal orifice along kidney almost to its apex. Mantle gland much less prominent than in *jousseaumei;* outer lung wall unpigmented.

Reproductive system (Figs 7A–B, 8C–D). Hermaphrodite gland comprising between five and seven lobes connected linearly to hermaphrodite duct, which bears clump of *culs-de-sac* and massively developed seminal vesicle (Fig. 8D). Talon short, simple and slightly curved; at its point of entry on spermoviduct is a large sac or caecum (Fig. 8C). Spermoviduct only slightly longer than free oviduct, which in turn is about twice length of vagina. Spermatheca with long, strong diverticulum which is continuous with basal stalk, and of equal thickness; spermatheca

Table 2 Tooth number and size from steroscan preparations and published data. Measurements are taken to the nearest 0·5 micron.

Species	Locality	No. per half row			Width	
		total	lat.	marg.	central	lateral
Euryptyxis candida	Taizz, 1979	40–42	13–14	26–28	26·0–26·5	28·0–28·5
	Menaha*	50	—	—	—	—
E. fragosa	Taizz, 1979	40–42	14–15	26–27	28·0–29·0	28·0–29·0
E. labiosa	Tawai Atair, 1978	31–33	13	18–20	28·0–28·5	29·0
E. latireflexa	Ain Arzat, 1976	39–41	13–15	26–27	23·0–23·5	23·0–24·0
	Tawai Atair, 1978	38–39	13	25–26	27·0–27·5	27·5–28·0
Cerastus schweinfurthi	Jabal Sumara, 1974	38	10	28	20·5	25·0
	Menaha*	43	—	—	—	—
C. scotti	Jebel Jihaf, 1937†	33	—	—	—	—
C. girwanensis	Jebel Girwan, 1938†	23	—	—	—	—
Zebrinops albatus	Taizz, 1978	26–27	10	16–17	16·5–17·0	19·0–19·5
	Taizz, 1937†	38	—	—	—	—
Z. 'ventricosa'	Dhala, 1937†	29	10	19	—	—
Imparietula jousseaumei	Rostaq, 1976	26–27	10	16–17	21·0–22·0	24·5–25·0
Mastus omanensis	Yika, 1976	24–26	11–12	13–15	11·0–12·0	13·5–14·0

*from Hesse, 1933
†from Connolly, 1941

proper continues as thin side-branch with large, globular head. Inserting at base of vagina and atrium is well-developed atrial retractor muscle.

Epiphallus inserting on penis apically with short flagellum at point of entry of vas deferens. A short retractor muscle inserts laterally on penis, and originates on lower lung wall. Within penis is a hollow papilla or verge occupying most of lumen (Fig. 7B), resembling Hesse's figure of the penial papilla of *Mastus pupa* (Hesse, 1933: fig. 2D). Penial appendix absent.

Two spermatophores were recovered and were closely similar in size and shape (Fig. 9B). Spermatophore approximately 10 mm long and 0·3–0·4 mm wide; pointed at anterior end and bearing a complex spiral fin at other. Rich corneous brown in colour. Both recovered from within spermatheca, and oriented with pointed end inserted into diverticulum.

COMMENTS. The reproductive anatomy of *omanensis* appears sufficiently similar to that of *Mastus* to be included within that genus; although differing in lacking the short median epiphallar caecum of *Mastus pupa,* it does agree in possessing a relatively large penial papilla and a short, blunt terminal epiphallar flagellum.

Of related genera, *Adzharia* Hesse is characterised by an elongate flagellum on the epiphallus (Hesse, 1930: 158), and *Chondrula* Beck and *Swertzowia* Kobelt by apertural dentition, neither of which is found in *omanensis*.

Subfamily **ENINAE** Pilsbry & Cooke, 1914

DIAGNOSIS. Kidney orthurethrous; lung with short renal groove, but lacking rectal fold. Hermaphrodite duct with clump of culs-de-sac above seminal vesicle; spermoviduct with serous canal; penis with diverticulum.

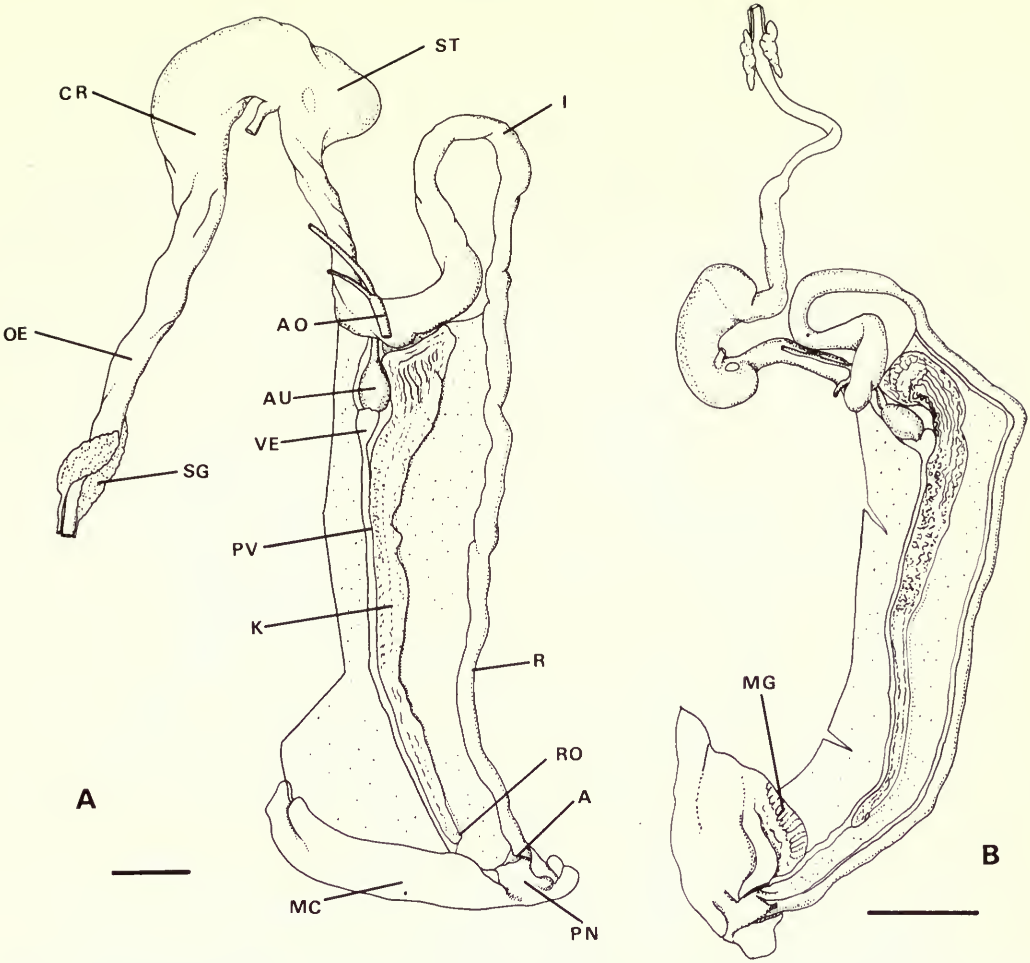


Fig. 6 Lung and alimentary system of A, *Mastus omanensis,* Yika, Oman, 1976; B, *Imparietula jousseaumei,* Saiq, Oman, 1980. Scale 2 mm.

Table 3 Length in whorls of the various regions of the visceral mass.

Species	Locality	Lung	Lung/ stomach	Stomach/ dig. gland	Total visc. mass	Shell
M. omanensis	Yika, 1976	1·1	1·1	2·4	4·6	5·9
	Ghafdi, 1976	1·2	1·1	2·5	4·8	6·0
I. jousseaumei	Ibri, 1977	1·8	1·2	3·4	6·5	7·0
	Saiq, 1981	1·9	1·1	2·5	5·5	6·2
E. candida	Taizz, 1979	1·2	0·7	2·6	4·5	6·8
E. fragosa	Taizz, 1979	0·8	1·1	2·4	4·3	7·0
	Taizz, 1946	1·1	0·9	2·7	4·7	7·4
E. labiosa	Tawi Atair, 1978	1·2	0·8	1·7	3·7	6·5
E. latireflexa	Ain Arzat, 1976	1·0	0·9	2·1	4·0	7·1
	Dahaq Thuari, 1977	1·3	1·0	1·6	3·9	6·7
Z. albata	Taizz, 1978	1·1	1·0	4·0	6·1	7·3

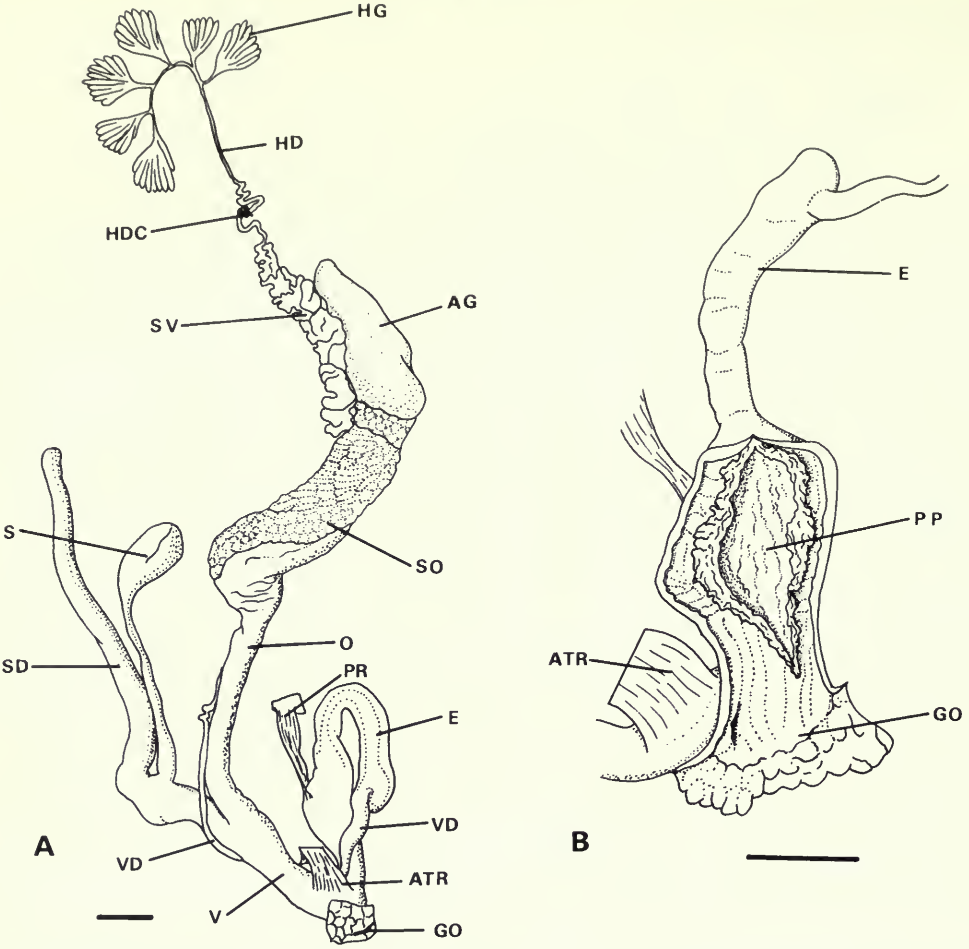


Fig. 7 *Mastus omanensis*, Yika, Oman, 1976: A, genital system; B, penis and epiphallus. Scale 1 mm.

IMPARIETULA Lindholm, 1925

(=*Pseudochondrula* Hesse, 1933)

Type species. *Bulimus leucodon* Pfeiffer [orig. desig.].

Diagnosis. Penis with appendix and short, blunt papilla; epiphallus with short median caecum. Spermatheca without diverticulum.

Imparietula jousseaumei (Smith, 1894)

Buliminus jousseaumei Smith, 1894:142, fig. 2. [Oman].
Buliminus (Subzebrinus) dautzenbergi Ancey, 1906:262. *Nom. nov. pro B. jousseaumei* Smith.
Buliminus jousseaumei Smith. Smythe & Gallagher, 1977:223.
Ena schahrudensis (Boettger). Smythe & Gallagher, 1977:223.

Type material. Lectotype (here selected, BMNH 1984.3.22.10) and Paralectotype (BMNH 1894.3.22.11); 5 possible Paralectotypes, mixed with the former (BMNH 1900.8.8.69–73), ‘Oman’, leg. Jayakar.

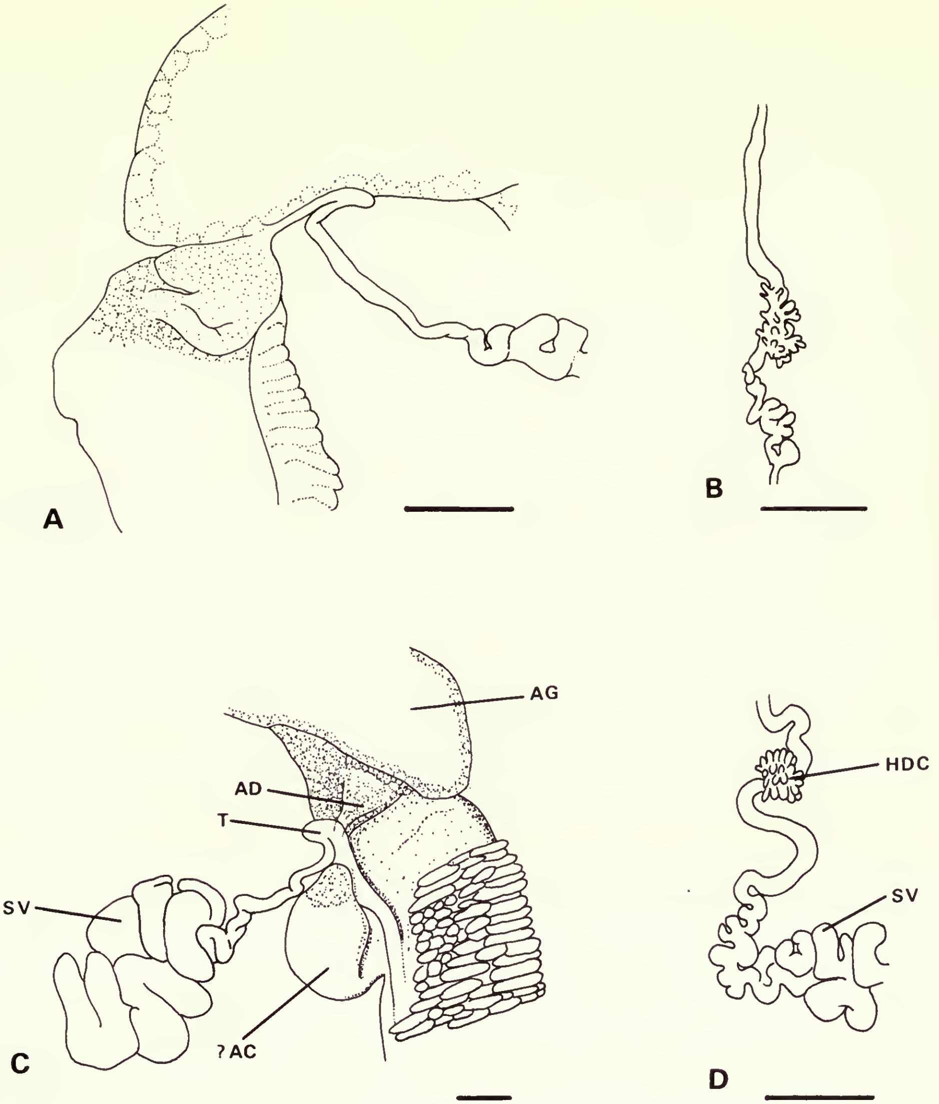


Fig. 8 *Imparietula jousseaumei,* Saiq, Oman, 1980: A, talon region; B, hermaphrodite duct. *Mastus omanensis,* Yika, Oman, 1976. C, talon region; D, hermaphrodite duct. Scale 0·5 mm.

OTHER MATERIAL. **Oman:** Mazra Qid, 488 m., leg. M. D. Gallagher, 15.xi.1976, BMNH, (9 specs., 2 dissected); Rostaq, 350 m., leg. M. D. Gallagher, 17.xi.1976, BMNH, (13 specs, 1 dissected); leg. R. P. Whitcombe, 12.ii.1979, (3 specs., spirit); Yika, c. 400 m., leg. M. D. Gallagher, 19.xi.1976, BMNH, (numerous specs., 2 dissected); Shafdi, Wadi Bani Ghafir, leg. M. D. Gallagher, 20.ix.1976, BMNH, (1 spec., spirit); Ibri, leg. M. D. Gallagher, 24.xi.1977, BMNH, (numerous specs., 1 dissected); Jabal Sira, 2200 m., leg, M. D. Gallagher, 12.vii.1977, BMNH, (8 specs.); 15.iv.1978, BMNH, (numerous specs., 4 spirit, 1 dissected); Sulaif, leg. M. D. Gallagher, 24.xi.1977, (6 specs.); Wadi Hilm, 100 m., leg. M. D. Gallagher, 15.iv.1978, BMNH, (3 specs.); Wadi Harabin, Eastern Hajar Mts., 125 m., leg. M. D. Gallagher & D. P. Mallon, 26.x.1979, BMNH, (numerous specs.); Jabal Kawr, 2800 m., leg. R. P. Whitcomb, 22.x.1979, BMNH, (3 specs.); Mudaybi, 300 m., leg. M. D. Gallagher & D. P. Mallon, 5.xi.1979, (1 spec.); Jabal Sham, 2980 m., leg. M. D. Gallagher, 20.i.1980, BMNH, (11 specs.); Wakan, 1400 m., leg. D. P. Mallon, 15.ii.1980, BMNH, (4 specs.); Saiq Camp, 1980 m., leg. T. Larsen & M. D. Gallagher, 22.v.1980,

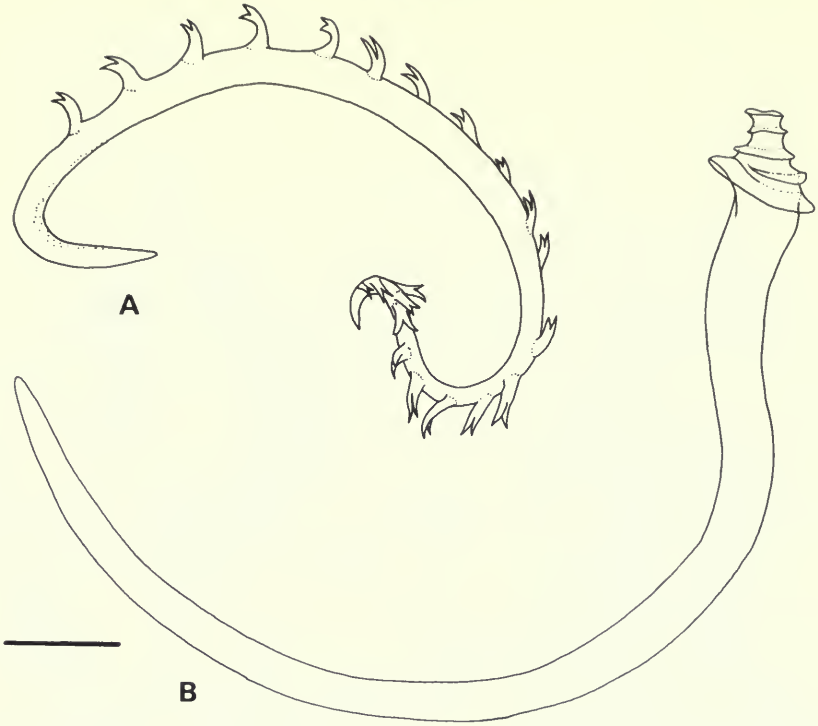


Fig. 9 Spermatophores: A, *Zebrinops albata*, Taizz, Yemen, 1978; B, *Mastus omanensis*, Yika, Oman, 1976. Scale 1 mm.

BMNH, (numerous specs., 3 dissected); leg. M. D. Gallagher, 21.v.1981, 1800–1860 m., BMNH, (numerous specs.); Jabal Aswad, Sharqiya, 1850 m., leg. M. D. Gallagher, 8.iii.1980, BMNH, (5 specs.); Tanuf, 600 m., leg. M. D. Gallagher, 20.iii.1981, BMNH, (5 specs.); Wadi Far, near Rostaq, leg. R. M. Lawton, ii.1982, BMNH, (1 spec.); Wadi Duwaykhilah, 1800 m., leg. M. D. Gallagher, 12.iii.1982, BMNH, (9 specs.); Wakan, 1500 m., leg. M. D. Gallagher, 26.iii.1982, BMNH, (numerous specs.).

DISTRIBUTION (Fig. 10). Widely distributed in the northern Oman mountains from the summit of Jabal Akhdar (2980 m) to the foothills; also recorded at a number of lowland synanthropic habitats down to 100 m in the eastern Hajar Mountains. It has not been recorded from Jebel Harim.

DESCRIPTION. Dextral, elongate pupiform, with tapering blunt apex; surface glossy with fine irregular transverse striae and occasional faint spiral striae; protoconch smooth and glossy. *Distinct columellar fold in the body whorl.* Whorls slightly rounded sutures shallowly impressed; umbilicus closed. Aperature oval; lip reflected and flattened, sometimes slightly reflexed at margin, *continuous across parietal wall and internally notched at the parietal/palatal junction. Colour transparent pale brown with irregular transverse opaque white streaks becoming progressively thicker towards the aperature*; protoconch brown; lip white.

Shell. Dimensions of Lectotype (Fig. 4b): 12·1 × 5·3 × 4·5; 4·8 × 3·9; lip 0·8; 7 wh. Remaining type series: 10·7 × 5·5 × 4·9; 4·7 × 4·0; lip 0·8; 6·2 wh.; 12·4 × 5·3 × 4·6; 4·9 × 3·9; lip 1·0; 7 wh.; 11·2 × 5·3 × 4·6; 5·0 × 3·9; lip 0·8; 6·4 wh.; 11·4 × 5·0 × 4·4; 4·5 × 3·7; lip 0·8; 6·4 wh.; 11·9 × 5·4 × 4·8; 4·8 × 3·6; lip 0·8; 6·7 wh.; 10·9 × 5·4 × 4·8; 4·8 × 4·1; lip 0·8; 6·3 wh.

This species appears to show rather greater geographical variation in shell morphology than *Mastus omanensis*, whilst maintaining considerable within-population homogeneity. Six living

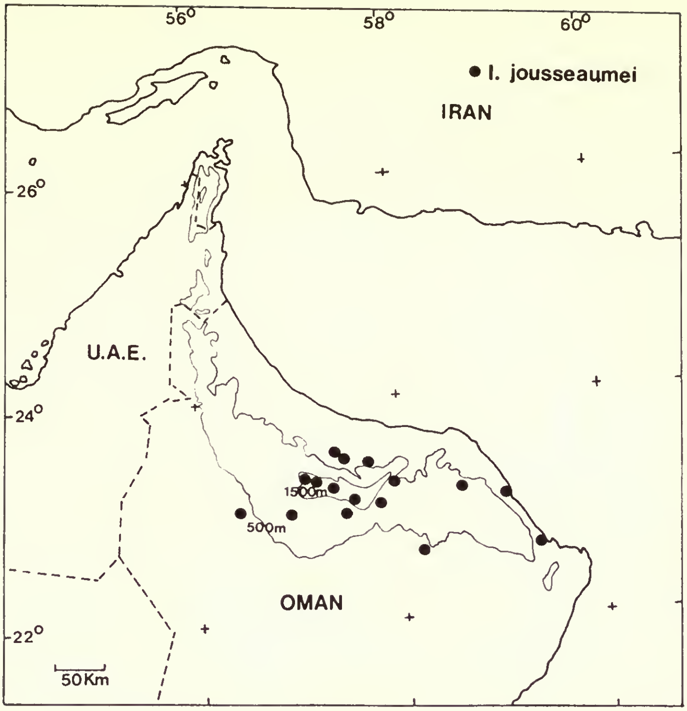


Fig. 10 Distribution map of *Imparietula jousseaumei.*

populations were examined, using analysis of variance (Table 4), the results proving significant for all shell parameters.

Body. Surface pale, almost colourless, but top of tubercules may be 'peppered' with grey or brown pigmentation.

Radula (Figs 5c–d). Teeth relatively slender in comparison with *Mastus omanensis* but only slightly fewer in number (Table 2). Unlike *omanensis*, marginal ectocones of *jousseaumei* commonly develop multiple cusps.

Lung cavity (Fig. 6B). Of the typical enid type with only a weak groove leading from renal pore to about half-way back along kidney margin. Kidney extends about 0·8 times length of entire lung. Venation very weak and bearly visible, but well-developed mantle gland present. Total lung cavity occupies 1·8–1·9 whorls (Table 3).

Reproductive system (Figs 8A–B, 11). Hermaphrodite gland composed of three or four lobes imbedded in digestive gland; duct bears clump of *culs-de-sac* above seminal vesicle (Fig. 8B), and terminates as talon formed from simple convolution of duct without any appendages. At point of entry of talon is a large sacculate structure (Fig. 8A) as in *Mastus omanensis*, similar to the albumen chamber of *Orcula* (Steenberg, 1925: pl. VIII). Albumen gland relatively short, about 2/3 length of spermoviduct, and about half length of the simple spermatheca. Epiphallus greatly modified, bearing blunt caecum about half-way along its length and a short terminal flagellum. Spermatophore unknown but epiphallus internally complex (Fig. 11B). Epiphallus enters penis apically through rounded papilla.

Penis has six, symmetrically arranged longitudinal pilasters, each with enlarged portion at top, separated from main body of pilaster by slight constriction; penis waisted at this point. Tops of pilasters form six-pointed coronet on tip of everted penis (Fig. 11C). Retractor muscle inserts laterally about half-way down penis on opposite side to appendix; latter of typical pupillacean

Table 4 Comparison of shell dimensions of living *Imparietula jousseaumei* from sites in northern Oman using Analysis of Variance.

	Yika, 19.xi.76 400 m.	(n=10)	J. Sira, 2750 m.	15.vi.78 (n=7)	Ibri, 24.xi.77 600 m.	(n=10)	Saiq, 22.v.81 1980 m.	(n=7)	Rostaq, 17.xi.76 350 m.	(n=6)	Wakan, 22.iii.82 1500 m.	(n=7)	F
Parameter	x	s.d.	x	s.d.	x	s.d.	x	s.d.	x	s.d.	x	s.d.	(d.f.=5,41)
Shell ht.	11·35	0·31	11·9	0·44	11·58	0·6	10·97	0·46	11·21	0·58	12·58	1·15	3·67**
Shell diam.	5·02	0·12	4·54	0·25	5·2	0·38	4·6	0·29	4·46	0·36	5·46	0·36	9·17***
Apert. ht.	4·36	0·19	4·14	0·18	4·58	0·25	4·15	0·09	4·41	0·25	4·45	0·34	4·02**
Apert. diam.	3·48	0·26	3·3	0·25	3·64	0·18	3·27	0·1	3·63	0·19	3·5	0·29	3·28*
Spire Index	2·27	0·22	2·61	0·11	2·31	0·2	2·4	0·24	2·1	0·15	2·3	0·09	5·41***

***$p < 0{\cdot}001$
**$p < 0{\cdot}01$
*$p < 0{\cdot}05$

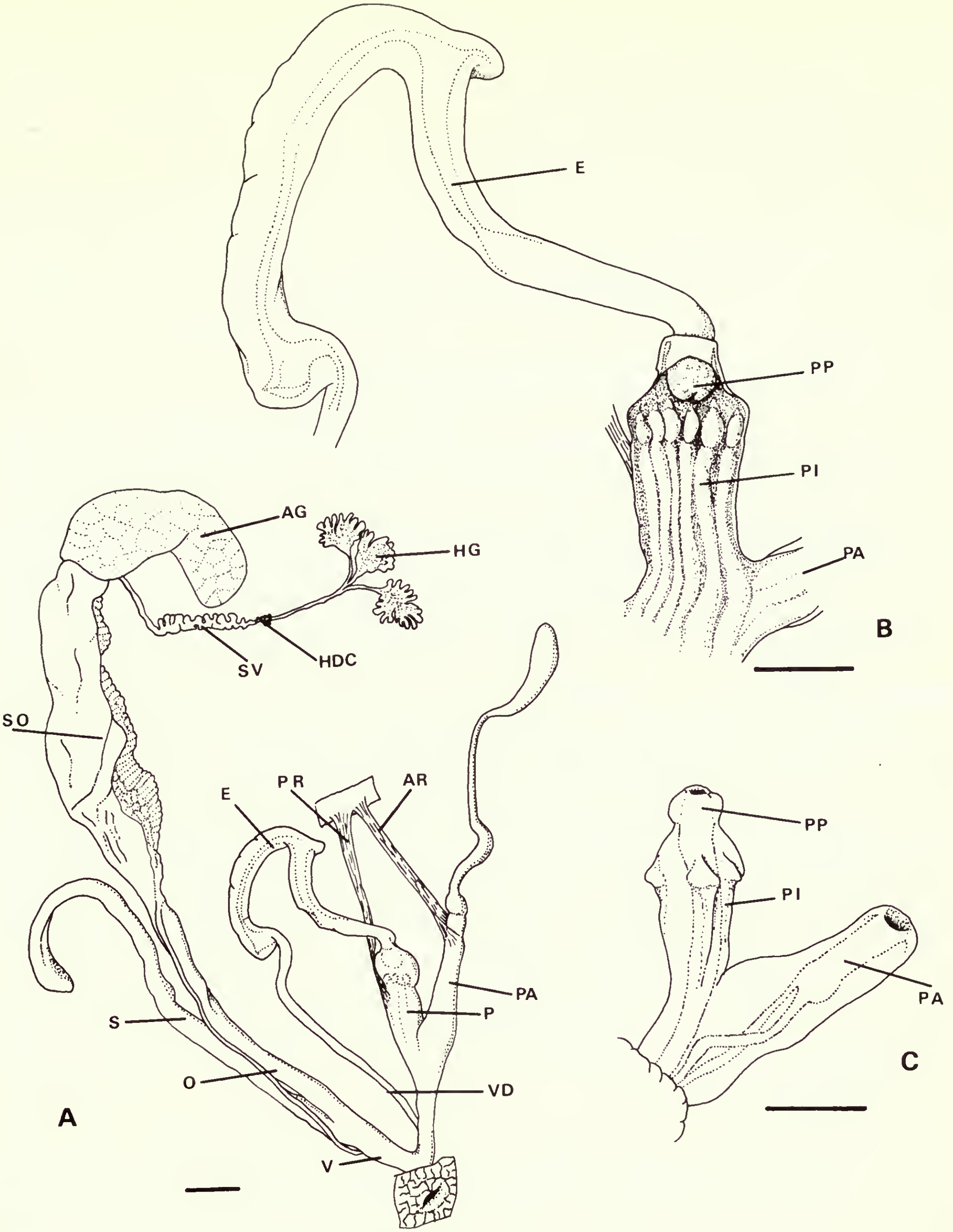


Fig. 11 *Imparietula jousseaumei,* Saiq, Oman, 1980: A, genital system; B, penis and epiphallus; C, everted genitalia. Scale 1 mm.

structure but relatively short (about 3–4 times length of penis). Appendicular retractor muscle inserts slightly below top of basal portion and originates next to but separate from penis retractor, on lower lung wall; base of appendix without strong pilasters. Atrium short and undifferentiated internally.

COMMENTS. The absence of a spermathecal diverticulum, combined with the presence of a penial appendix and an epiphallus with a short terminal flagellum and blunt median caecum, which inserts apically on the penis, place this species within *Imparietula*. Conchologically it is quite distinct from any other named species of the genus (Forcart, 1940; Gittenberger, 1967). Smythe & Gallagher's (1977: 223) record of *Ena schahrudensis* from Jabal Sham is erroneous, being merely an elongate form of *Imparietula jousseaumei*.

PARAMASTUS P. Hesse, 1933

TYPE SPECIES. *Bulimus episomus* Bourguignat [monotypy].

Paramastus episomus (Bourguignat, 1857)

Buliminus episomus Bourguignat, 1857: 10, pl. 3, figs 5–7. [Nazareth].
Buliminus hedjazicus Bourguignat, 1882: 24, pl. 1, fig. 12. [between Jeddah and Mecca].
Paramastus episoma hedjazicus Bourguignat. Zilch, 1951: 42, pl. 3a, fig. 16.
?*Paramastus episomus* Bourguignat. Mordan, 1980:360, fig. 2I.

TYPE MATERIAL. Holotype, Between Jeddah and Mecca, Saudi Arabia, MHNG.

DISTRIBUTION. Known only from the type locality (above).

DESCRIPTION. Dextral, pupiform; surface with weak, irregular radial striae and weaker, but more regular, spiral striae, and occasional malleations, especially on body whorl; umbilicus closed. Aperture elongate oval, with flared, sharp lip; small parietal denticle near palatal/parietal boarder, and weak, broad columellar fold. Shell opaque white, but periostracum lacking.

Shell. Dimensions of holotype (Fig. 4c): 15·2 × 6·5 × 6·4; 5·8 × 4·3; 6·7 wh.

Anatomy. Unknown.

COMMENTS. See below under *P. sabaeanus*.

Paramastus sabaeanus (Bourguignat, 1876)

Bulimus sabaeanus Bourguignat, 1876:19 [Sabéens, near Mareb.]; Bourguignat, 1882:23, fig. 14.
Buliminus (Petraeus) sabaeanus Bourguignat. Rossmässler, 1888:31, pl. 99, fig. 560. *non sabaeanus* (Bgt.) Rolle & Kobelt, *in* Rossmässler, 1895–97:58, pl. 11, figs 8–11.

TYPE MATERIAL. Lectotype (here selected) and Paralectotype, Sabéens, near Mareb, Yemen, MHNG.

DISTRIBUTION. Known only from the type locality (above).

DESCRIPTION. As for *hedjazicus*, but aperture relatively larger and rounder, with flattened lip; spiral striae and parietal denticle absent.

Shell. Dimensions of lectotype (Fig. 4d): 23·1 × 10·2 × 9·4; 9·5 × 7·0; 7·7 wh. Paralectotype: 21·7 × 10·0 × 8·8; 9·0 × 7·2; 7·5 wh.

Anatomy. Unknown.

COMMENTS. The positions of this and the previous taxon at both the specific and generic levels is uncertain. Until recently both would have been referred to *Paramastus* Hesse on conchological and geographic grounds. This is still the most likely eventuality and they are provisionally retained here. However, Heller (1971) has demonstrated that *Paramastus sensu lato* comprises two groups: one, which he named *Cyrenaicus*, lacking a penial appendix and with a distribution centered on Cyrenaica; and *Paramastus sensu stricto* possessing a penial appendix and containing with certainty only two species (*P. episomus* (Bourguignat, 1857) and *P. cyprius* Zilch, 1959). The true affinity of the Arabian snails is thus in doubt. Zilch (1951) relegated *hedjazicus* to a subspecies of *episomus* and this is retained here. Certainly both Arabian taxa fall broadly within the wide morphological range of *episomus*. Without anatomical information further speculation is valueless.

Subfamily *CERASTINAE* Wenz, 1923

DIAGNOSIS. Kidney orthurethrous; lung with well-developed renal and rectal folds. Hermaphrodite duct without culs-de-sac, and spermoviduct without serous canal. Penis with appendix.

CERASTUS Albers, 1860

TYPE SPECIES. *Bulimus distans* Pfeiffer [orig. desig.]

DIAGNOSIS. Shell lip undifferentiated or weakly flared. Penis with long, pointed caecum; penis retractor inserts on epiphallus. Penial appendix with moderately developed papilla; appendicular retractor inserts on enclosed basal portion of central stalk. Penial and appendicular retractors united prior to attachment to lung wall.

Cerastus schweinfurthi (Martens, 1895)

Buliminus schweinfurthi Martens, 1895:129. [Menaha].
Buliminus schweinfurthi var. *gracilior* Martens, 1895:129. [Menaha].
Buliminus (Cerastus) schweinfurthi Martens. Kobelt, 1902:893, pl. 127, figs 19–21; Rossmässler, 1903:51, pl. 291, fig. 1862.
Buliminus (Cerastus) schweinfurthi var. *menahensis* Kobelt, 1902:894, pl. 127, figs 22, 23. [Menaha].
Buliminus (Cerastus) schweinfurthi var. *menahensis* Kobelt. Rossmässler, 1903:52, pl. 291, fig. 1863.
Cerastus schweinfurthi Kobelt. Connolly, 1941:26.
Cerastus schweinfurthi var. *maxima* Connolly, 1941:26. [pass between Saiyani and Ibb].
Cerastua (Euryptyxis) schweinfurthi Martens. Hesse, 1933:220.
Cerastua schweinfurthii Kobelt. Verdcourt, 1974:5.
Cerastua schweinfurthii var. *maxima* Connolly. Verdcourt, 1974:5.

TYPE MATERIAL. Lectotype (here selected, BMNH 1895.8.20.1), Paralectotype (BMNH 1895.8.20.2), and 5 possible Paralectotypes (BMNH 1937.12.30.2127–31) of *schweinfirthi* Martens, Menaha, Yemen, leg. Schweinfurth. Holotype and 6 Paratypes (BMNH 1939.4.19.34–40) of var. *maxima* Connolly, Naqil Mahrras Pass, between Seyani to Ibb, Yemen, leg. Scott, 30.xii.1937, c. 2200 m.

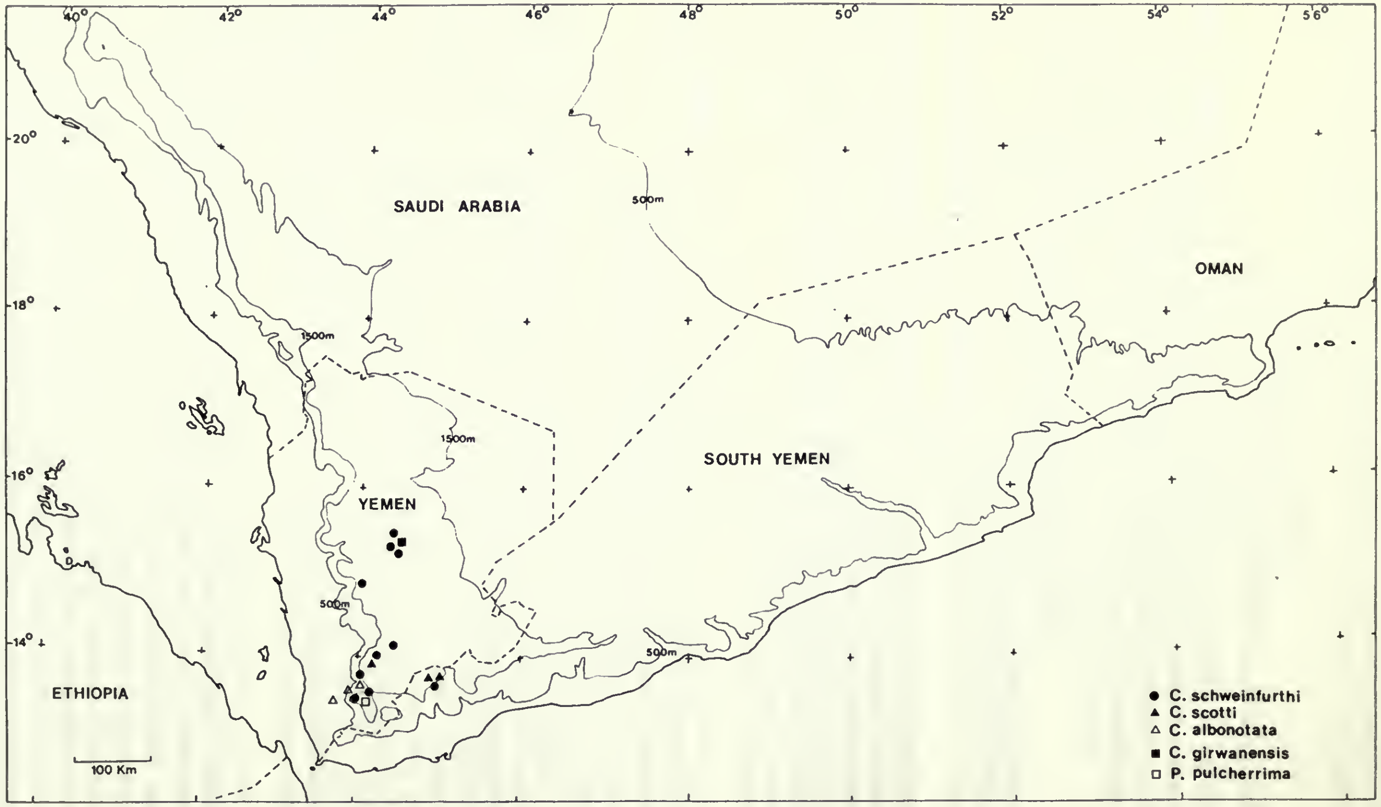
OTHER MATERIAL. **Yemen:** Taizz District, 1250–1550 m. leg. H. Scott, BMNH 1939.4.19.53–54 (2 specs.); Wadi Dhulla, 10 km. NW. Saana, 2500 m., Leg. H. Scott, BNMH 1939.4.19.41–42 (2 specs); Thawilah, leg. L. Merucci, vi.1945, BMNH 1956.11.26–30 (5 specs + 20 unregistered); 8 km from Taizz, leg. M. Brunt & J. Mather, (1 spec); Wadi Shabau, leg. Brunt & Mather, (2 specs.); As Saiyani, 32 km N Taizz, leg. Lavranos, 1977, MNHN (9 specs); 32 km. N. Sanaa, leg. M Al-Safadi, (1 spec); Jebel Sumara, north of Ibb, 2950 m., leg. M. Lavranos, 1974, MNHN, (5 specs., 1 reconstituted and dissected). **South Yemen:** Jebel Harir, x-xi.1937, 2300 m., 1 paratype *maxima* Connolly, BMNH 1939.4.19.27, leg. H. Scott.

DISTRIBUTION (Fig. 12). The species extends from near Dhala in South Yemen westwards to the region of Taizz, and northwards to the type locality of Menaha and to Sana. It is thus the most widely distributed Arabian *Cerastus,* and by far the most abundant in museum collections.

DESCRIPTION. Dextral; acuminate ovate, apex blunt, sutures shallow. Protoconch smooth, later with regular radial ribs; radial sculpture becoming progressively weaker, and in combination with spiral striae giving glossy appearance. Aperture not flared, slightly thickened internally, callus extending across parietal wall. Periostracum corneous olive-brown, variegated in occasional radial streaks of darker brown.

Shell. Dimensions of Lectotype, *schweinfurthi* von Martens (Fig. 13a): 31·4 × 17·4 × 1·1; 17·0 × 11·9; 7·1wh. Dimensions of holotype, var *maxima* Connolly (Fig. 13b): 47·3 × 26·5 × 23·4; 26·2 × 18·5; 7·8 wh. Largest specimen, Wadi Shabau, Yemen, leg. Brunt & Mather: 42·7 × 25·2 × 20·6; 24·4 × 17·3; 7·3 wh.

Cerastus schweinfurthi shows considerable variation in both shell size and shape, particularly in the region between Taizz and Ibb in Yemen, from where Connolly described var *maxima*. There was a general correlation between shell size and thickness, the very largest shells being up to 1·8 mm thick.


40°
42°
44°
46°
48°
50°
52°
54°
56°
20°
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16°
14°
SAUDI ARABIA
OMAN
YEMEN
SOUTH YEMEN
ETHIOPIA
500m
1500m
1500m
500m
500m
100 Km
● C. schweinfurthi
▲ C. scotti
△ C. albonotata
■ C. girwanensis
□ P. pulcherrima

Fig. 12 Distribution map of *Cerastus* and *Polychordia*.

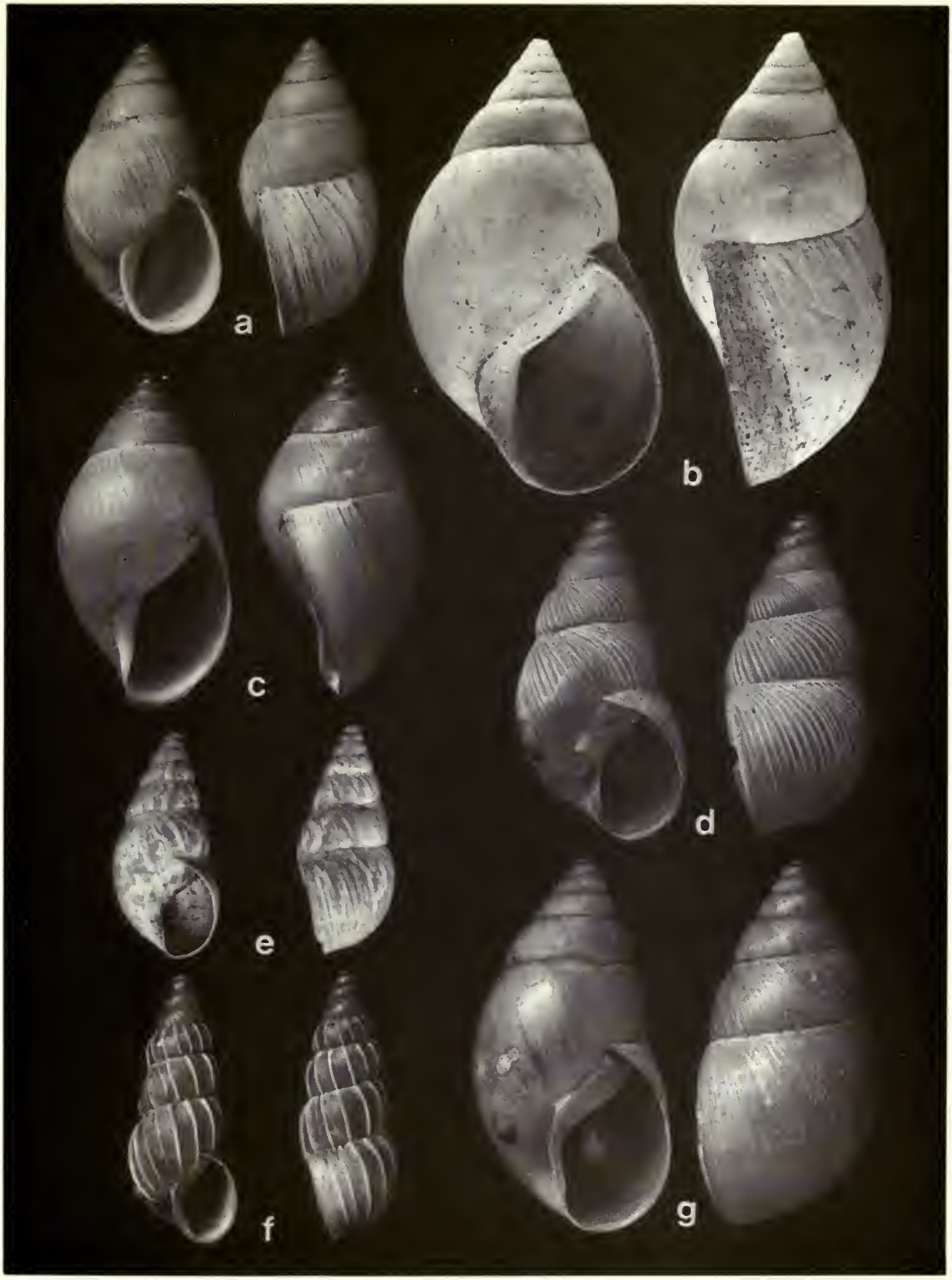


Fig. 13 a, Lectotype of *Buliminus schweinfurthi* Martens, BMNH 1895.8.20.1, × 1·5; b, holotype of *Cerastus schweinfurthi* var. *maxima* Connolly, BMNH 1939.4.19.34, × 1·5; c, paratype of *C. schweinfurthi* var. *maxima,* BMNH 1939.4.19.27, × 1·5; d, lectotype of *C. girwanensis* Connolly, BMNH 1934.4.19.9, × 3; e, holotype of *Cerastua albonotata* Verdcourt, BMNH 19731, × 1·5; f, holotype of *Polychordia pulcherrima* Connolly, BMNH 1939.4.19.55, × 3; g, holotype of *Cerastus scotti* Connolly, BMNH 1939.4.19.11, × 3.

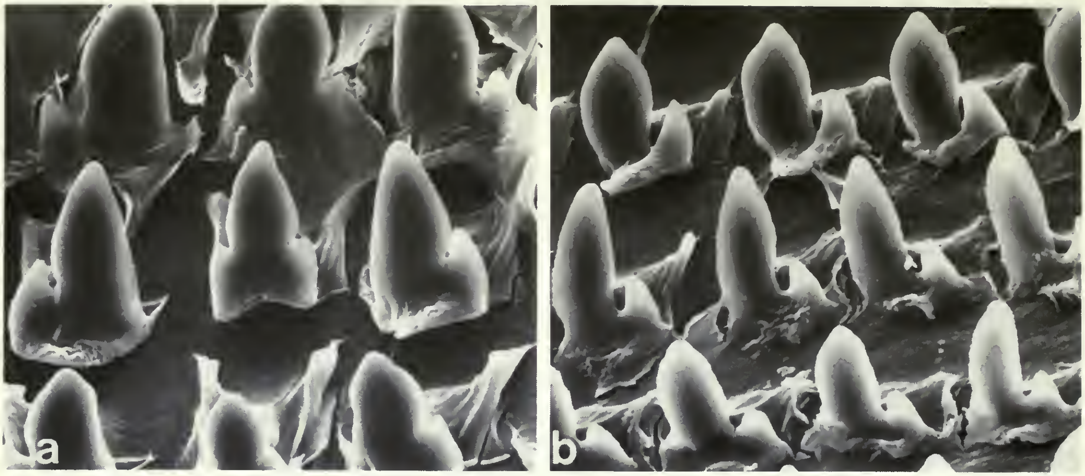


Fig. 14 Radula of *Cerastus schweinfurthi*, reconstituted specimen, Jebel Sumara, Yemen, 1974: a, central and lateral teeth; b, marginal teeth; × 720.

Body. Darkly pigmented in uniform browny-black.

Radula (Fig. 14; Table 2). Part of a radula was extracted from the reconstituted specimen. Although the teeth were immature, it was possible to confirm that in all teeth the mesocones are relatively elongate, and the bases narrow in comparison with *Euryptyxis*. The marginal ectocones have a single cusp, which appears to be lacking from the outermost teeth.

Lung cavity. As far as could be established, complete renal and rectal folds are developed, united at the top of the lung. The kidney is 0·85 times the cavity length, and venation is noticeably more prominent near the mantle collar. The outer lung wall is dark brown/black with irregular patches and streaks of opaque white.

Reproductive system (Fig. 15). Hesse (1933:220–221, fig. 43.) has figured the reproductive system of *Cerastus schweinfurthi* and also gave a comprehensive description of its gross morphology. Three important features of this description are: the spermatheca which is clearly separated into head and stalk regions, the well-developed, elongate penial caecum; and the penis retractor muscle which is united with the appendicular retractor for some distance after its origin on the lower lung wall, and which inserts singly on the epiphallus. Hesse also figures a spermatophore, and a detail of a single spermatophore 'scale' (Hesse, 1933: fig. 43, D–E).

Only a single, reconstituted specimen was available for dissection in the present study. From this, it has been able to confirm many features of Hesse's description, and also describe in more detail the internal morphology of the penial appendix. It is clear (Fig. 15A) that the morphology of the junction of the basal and middle portions of the appendix is similar to *Zebrinops* although the projection of the papilla into the basal lumen is shorter. Additionally, the penial muscle sheath is single-layered. Internally, the epiphallus appeared to have spiral ornamentation and Hesse states that there is a single row of 'scales' on the spermatophore, which appears to be spirally arranged in his figure.

COMMENTS. The shell of *schweinfurthi* most closely resembles that of *Cerastus scotti* but is readily separable by its much greater size; the two species co-occur at Jebel Harir, near Dhala, South Yemen.

Cerastus albonotatus (Verdcourt, 1974)

Cerastua albonotata Verdcourt, 1974:5, figs 2a–c.

TYPE MATERIAL. Holotype, BMNH 19731, 5 miles out of Taizz, Yemen, ix.1971, leg. M. Brunt & J. D. Mather.

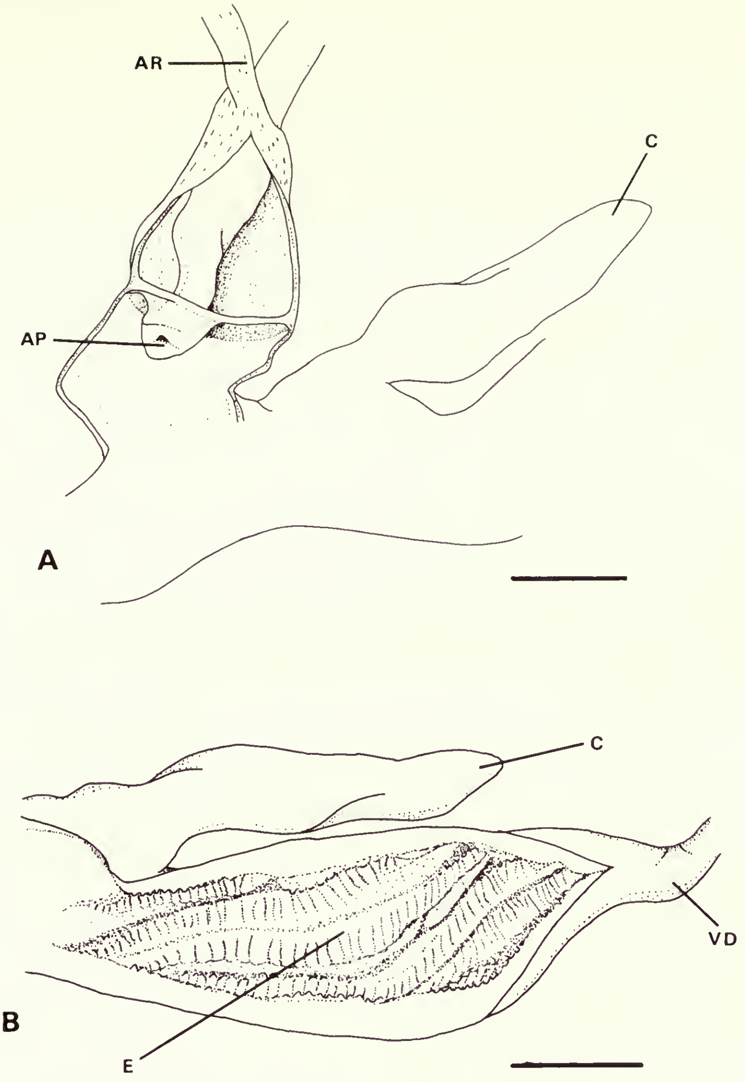


Fig. 15 *Cerastus schweinfurthi*, J. Sumara, Yemen, 1974 (Reconstituted specimen). A. Base of penial appendix; B. Epiphallus. Scale 1 mm.

Other material. **Yemen:** Wadi 20 miles east of Taizz, leg. Waterson, (1 spec.) Near Taizz, 1978, leg. P. Heath, (2 specs.).

Distribution (Fig. 12). Known only from the vicinity of Taizz, Yemen.

Description. Dextral; elongate conical; *ribs wavy, irregularly spaced and of varying thickness even within a single rib,* 2–3 ribs per mm. on body whorl; spiral striae absent; protoconch initially smooth, later with close, regular, sharp, straight ribbing. Sutures deep; narrow, shallow umbilicus; aperture sharp and unthickened. Colour pale brown, *with irregular, predominantly radial streaks or flammulations of opaque white.*

Shell. Dimensions of Holotype (Fig. 13e): 18·2 × 8·8 × 7·6; 7·7 × 5·5; 8·8 wh. The holotype is the largest of the four known specimens.

Anatomy. Unknown.

COMMENTS. Although the material is limited, it does show remarkable uniformity in shell form, and in view of the similar lack of conchological variability in the other small Arabian species of *Cerastus,* must be considered a valid taxon. Morphologically, the shell is closest to that of *girwanensis* from which it differs principally in the details of its ribbing and colouration.

Cerastus girwanensis Connolly, 1941

Cerastus girwanensis Connolly, 1941:27, pl. 3, fig. 13.

TYPE MATERIAL. Lectotype (here selected, BMNH 1939.4.19.9) and Paralectotype (BMNH 1939.4.19.10), Jebel Girwan, Yemen, 2700 m., leg. P. W. R. Petrie, 17.ii.1938.

DISTRIBUTION (Fig. 12). Known only from the type locality, Jebel Girwan, near Ghaiman, about 17 km SE. of Sana, Yemen.

DESCRIPTION. Dextral; elongate conic; apex blunt, sutures deep; protoconch initially smooth becoming ribbed, *ribbing regularly spaced, sharp and of even thickness (2–3 ribs/mm.),* spiral striae absent. Umbilicus narrow and shallow, aperture sharp, unthickened. Colour uniform pale brown, ribs paler.

Shell. Dimensions of Lectotype (Fig. 13d): 17·0 × 9·5 × 8·0; 7·6 × 5·2; 7 wh.

Anatomy. The radula and jaw of the smaller, immature, type were described by Connolly (1941:28); the radula closely resembles that of *C. scotti* but had considerably fewer teeth (Table 2). Like *scotti* the marginal ectocones were multicuspid in all but the first two teeth.

COMMENTS. See *C. albonotatus* above.

Cerastus scotti Connolly, 1941

Cerastus scotti Connolly, 1941:22, pl. 3, fig. 14, text fig. 7. [Jebel Jihaf].

TYPE MATERIAL. Holotype (BMNH 1939.4.19.11) and 6 paratypes (BMNH 1939.4.19.12–17), Jebel Jihaf, South Yemen, 2000–2300 m; 2 paratypes, Jebel Harir, South Yemen, BMNH, leg. Scott & Britton, x–xi. 1937.

OTHER MATERIAL. **Yemen:** Naqd Al Ahmar, between Ibb and Taizz, 2400 m., 25.ix.1977, leg Lavranos. **South Yemen:** Jebel Jihaf, 2000–2300 m., x–xi. 1937, leg. Scott & Britton, (4 specs.).

DISTRIBUTION (Fig. 12). Recorded from elevated sites in the region of Taizz, Yemen and Dhala, South Yemen, and it is thus more widely distributed than other small *Cerastus* species.

DESCRIPTION. Dextral; *elongate ovoid*; ribs fine, initally strong and regularly spaced, *becoming much weaker and less regular (6–9 ribs/mm.)*; weak spiral striae giving glossy surface appearance. Apex sharp, protoconch initially smooth; *sutures not deeply impressed*; narrow, shallow umbilicus; aperture sharp, unthickened. Colourless to very pale brown, semi-transparent; stronger early ribs may be translucent white.

Shell. Dimensions of Lectotype (Fig. 13g): 19·3 × 10·6 × 9·1; 9·6 × 6·2; 6·9 wh. Largest specimen: Naqd al Ahmar, Yemen: 22·7 × 11·1 × 9·8; 10·0 × 6·6; 8 wh.

Anatomy. The jaw and radula were described by Connolly (1941:27, fig. 7); see Table 2. The remaining anatomy is unknown.

COMMENTS. *C. scotti* differs from the other small Arabian *Cerastua* by its shell shape and ribbing, resembling a small *C. schweinfurthi.* It is easily separated from the latter by its considerably smaller size for an equivalent number of whorls.

POLYCHORDIA Connolly, 1941

TYPE SPECIES. *Polychordia pulcherrima* Connolly [monotypy].

DIAGNOSIS. Shell as in *Crerastus* but more elongate with deeper sutures; costae thin and raised, regularly and widely spaced.

Polychordia pulcherrima Connolly, 1941

Polychordia pulcherrima Connolly, 1941:28, pl. 3, fig. 10.

TYPE MATERIAL. Holotype (BMNH 1939.4.19.55) and 10 paratypes (BMNH 1939.4.19.56–65), Wadi Thabad, north slope of Jebel Sabir, Yemen, c. 1800 m., 25–26.xii.1937, leg. Scott & Britton. 31 additional possible paratypes, as above, BMNH.

DISTRIBUTION (Fig. 12). Known only from the type locality at Jebel Sabir, near Taizz, Yemen.

DESCRIPTION. Dextral; elongate conical, apex blunt, sutures deep, whorls rather shouldered in profile, umbilicus narrow and shallow; protoconch initially smooth, becoming regularly ribbed, *ribs very prominent and sharp, regularly and widely spaced.* Aperture sharp, unthickened. Colour pale brown, translucent, ribs opaque white.

Shell. Dimensions of Holotype (Fig. 13f): 13·8 × 5·2 × 4·8; 4·7 × 3·3; 8 wh. Largest paratype: 15·9 × 5·8 × 5·3; 4·8 × 3·3; 8·1 wh.

Anatomy. Unknown.

COMMENTS. The shell is closest to that of *Cerastua girwanensis,* but differs in the strength and spacing of the ribbing. Connolly's original generic positioning is retained although it is probable that once the anatomy is known this species will be found to be a *Cerastus.*

EURYPTYXIS P. Fischer, 1883

TYPE SPECIES. *Pupa candida* Lamarck [monotypy].

DIAGNOSIS. Shell with clearly developed flared lip. Penis with short, rounded caecum; penial retractor with multiple insertion on penis and epiphallus in Arabian forms. Penial appendix with short, blunt papilla; appendicular retractor inserts at junction of basal and central portions of the appendix; base of central stalk not enclosed. Origin of penial and appendicular retractors separate or adjacent.

Euryptyxis candida (Lamarck, 1822)

?*Helix arabica* Forskal, 1775:127. [Loharjae], *nomen dubium.*
Helix sulcata Müller [*pars*]. Martini & Chemnitz, 1786:165, pl. 135, fig. 1231.
Pupa candida Lamarck, 1822:106. [loc. unknown]; 1833:171.
Buliminus forskalii Beck, 1837:68. [Arabia].
Pupa candida Lamarck. Delessert, 1847:pl. 27, figs 10a–b.
Buliminus forskalii Beck. Pfeiffer, 1842:45; Kuster & Pfeiffer, 1845–55: 49, pl. 15, figs 6, 7, pl. 18, figs 3, 4; Reeve, 1849:pl. LXI, species 419; Westerlund, 1887:64.
Pupa arata Récluz, 1843*a*:4; 1843*b*:pl. 75. [Socotra].
Bulimus fragosus Férussac. Reeve, 1849:pl. LXIV, species 446.
Bulimus candidus Deshayes. Férussac & Deshayes, 1851:77, pl. 150, figs 15, 16;
Buliminus candidus Lamarck. Rossmässler, 1880:41, pl. 198, fig. 1984; Westerlund, 1887:64.
Bulimus candidus Lamarck. Paladilhe, 1872:pl.1, fig. 17. Bourguignat, 1882: 16, figs 6–8.
Bulimus micraulaxus Bourguignat, 1882, 17, fig. 20. [Southern Arabia].
Buliminus eryx Westerlund, 1887:64. [Arabia].
Buliminus (Petraeus) eryx Westerlund. Rossmässler, 1888:31, pl. 99, fig. 559; Kobelt, 1902:402, pl. 71, figs 11, 12.
Buliminus (Petraeus) candidus Lamarck. Kobelt, 1902:407, pl. 72, figs 2, 3.
Euryptyxis forskalii Pfeiffer. Connolly, 1941:30; Verdcourt, 1974:8.
Pupa candida Lamarck. Mermod, 1951:717, fig. 71.
Euryptyxis candida Lamarck. Verdcourt, 1974:6; Mordan, 1980*a*: 360, fig. 2k.

TYPE MATERIAL. Possible Syntypes of *arata* Récluz, 'Yemen', Petit Collection, BMNH 1943.10.2.53–55, (3 specs.).

The Lamarck types of *candida* have not been examined but a representative specimen is well illustrated by Mermod (1951, Fig. 71), leaving no doubt as to the identity of the species. The name *Helix arabica* Forskäl predates *candida* but is here considered a *nomen dubium.* It is based on material collected by Forskäl himself which is now housed in the Copenhagen Museum (together with the material which forms the basis of the accounts of Martini and Chemnitz (1786) and Beck (1837)). The original description of *arabica* refers to a smooth, white shell ('*alba*' and '*glabra*'), whereas the specimens purporting to be the types are strongly ribbed (Fig. 16d) as in typical *candida*, and are mostly pale brown in colour. The description better fits *labiosa* Müller, and the true identity of *arabica* Forskäl is clearly uncertain.

One specimen of *candida* from the Spengler collection, ZMC, is probably the original of a poor figure labelled *Helix sulcata* Müller in Martini and Chemnitz (1786, fig. 1231). This figure is cited as an indication by Beck (1837) for the name *Buliminus forskalii* and thus the Spengler specimen is most likely the type of *forskalii* Beck.

OTHER MATERIAL. **Yemen:** Ibb, leg. Haythornthwate, BMNH 1935.4.4.34, (1 spec.); 10 miles N. Zabid, leg. A. R. Waterson, 15.xii.1945, RSM 1953.52.105, (11 specs.); Wadi Rema, 1250 m., leg. A. R. Waterson, 2.ix.1946, RSM 1953.52.104, (2 specs.); Wadi Ja'ira, leg. A. R. Waterson, 4.ix.1946, RSM 1953.52.112, (4 specs); Wadi Hamman, 1700 m., leg. A. R. Waterson, 2.ix.1946, RSM 1953.52.107, (1 spec.); Wadi Thaban, N. side of Jebel Sabir, c 1850 m., leg H. Scott, BMNH 1939.19.43–45, (3 specs.); Wadi Dharh, NW. Sana, c 2500 m., leg. P. W. R. Petrie, vii.1938, BMNH, (4 specs.); 5 miles Taizz, leg. M. A. Brunt & J. D. Mather, xi.1971, BMNH, (2 specs); Wadi Zabid, leg. M. A. Brunt & J. D. Mather, BMNH, (8 specs.); 34 km. N. Taizz, leg. J. Lavranos, 1978, MNHN, (3 specs); As Saiyani, 32 km. N. Taizz, leg. M. Lavranos, 1977, MNHN, (1 spec.); Wadi Shadhb, 30 km. W. Menakha, 1400 m., leg. M. Lavranos, 1977, MNHN, (12 specs.); Al Maghriba, 2300 m, leg. M. Lavranos, 1977, MNHN, (2 specs); 20 miles N. Sana, Leg. M. Al-Safad, 1979, BMNH, (3 specs.); Taizz, 1400 m., Leg. P. Heath, iv.1978, BMNH 1982, (3 specs, 2 dissected); Al Hyma, near Taizz, 1100 m., Leg. P. Heath, ix. 1979, BMNH 1982, (3 specs, 2 dissected); Al Gharabi, Tihama, leg. M. D. Gallagher, 28.xi.1982, BMNH, (11 specs). **South Yemen:** near Dhala, leg. D. W. Bury, BMNH 1903.7.6.5–6, (2 specs.); Wadi Dareija, near Dhala, 1400 m., leg. H. Scott, BMNH 1939.4.19.19–20, (2 specs.); Dhala, over 1550 m., Leg. H. Scott, BMNH 1939.4.19.26, (1 spec.); Jebel Jihal, 1920–2200 m., leg. H. Scott, BMNH 1939.4.19.29–33, (5 specs.); Wadi Tiban, Musemir, leg. Petrie, BMNH 19407.13.24–26, (3 specs.). **Saudi Arabia:** East Cape, Dumsuk island, Farsan Islands, leg. W. A. Macfadyen, BMNH 1928.3.16.33–47, (15 specs.); Farsan Islands, leg. G. W. Young, BMNH 1931.4.25.83–84, (2 specs); Wadi Muhaishira, Jadaliya, leg. H. St. J. B. Philby, 17.i.1936, BMNH, (1 spec.); Suq Aiban, leg. H. St. J. B. Philby, 21.xii.1936, BMNH, (5 specs.); Math'an Plain, leg. H. St. J. B. Philby, 21.xii.1936, BMNH, (8 specs.); Wadi near Khamis Mishat, leg. A. R. Waterson, 24.viii.1944, BMNH 1945.8.23.187–190, (4 specs.); RSM 1953.52.115, (9 specs.); 10 miles N. Amk, Tihama, leg. A. R. Waterson, 14.ix.1944, RSM 1953.52.109, (4 specs.); Wadi Damat, Tihama, leg. A. R. Waterson, 14.iii.1945, RSM 1953.52.110, (1 spec.); ?Suda, leg. J. D. Toothill, BMNH 1952.10.30.55, (1 spec.); 65 km from Najran, on road to Abha, leg. J. Lavranos, 1980, MNHN (10 specs); Abu Arish, nr. Jizan, leg. Lavranos, 1980, MNHN (numerous); Wadi Manfar, Najran, leg. Lavranos, MNHN (1 spec.); Wadi Kharra, leg. K. Gotto Smith, 10.xi.1982, BMNH, (1 spec.).

DISTRIBUTION (Fig. 17). Restricted to the south-west of Arabia. The range is similar to that of *E. fragosa*, but extends further northwards into the Asir province of Saudi Arabia, and westwards to the Farsan Islands in the Red sea. The southern- and eastern-most localities are respectively near Musaymir and in the region of Dhala, both in South Yemen. A number of early records are from Socotra, but these have not been confirmed in recent years.

DESCRIPTION. Dextral; pupiform, surface with strong sharp *regular radial ribs*, and very fine, wavy spiral striae which cross the ribbing; protoconch initially smooth becoming radially ribbed; umbilicus closed. Aperture with *flared lip, never recurved*, and often thickened just internal to the margin; *strong internal columellar fold in body whorl* (Fig. 18D), not visible from aperture. Colourless opaque to brown, lip may be more deeply pigmented.

Shell. Dimensions of figured syntype *candida* Lamarck (Mermod, 1951:717, fig. 71): shell height 24·5; shell diam. 13·0; apert. height 12·0; whorls 7·5. Syntypes *arata* Récluz: 25·9 × 13·4 × 12·1; 12·9 × 9·4; lip 1·9; 7·7 wh.; 25·4 × 13·1 × 11·9; 13·2 × 10·1; lip 1·8; 7·6 wh.; 25·7 × 13·5 × 11·2; 13·1 × 9·4; lip 2·1; 7·7 wh. Largest specimen, Dhala, South Yemen, leg H. Scott (Fig. 16a): 40·1 × 19·9 × 16·1; 18·5 × 14·0; lip 3·4; 8·9 wh. Smallest specimen, Dumsuk Island, Red Sea, leg Macfadyen (Fig. 16c): 16·8 × 10·0 × 8·2; 9·8 × 6·2; lip 1·0; 6·4 wh.

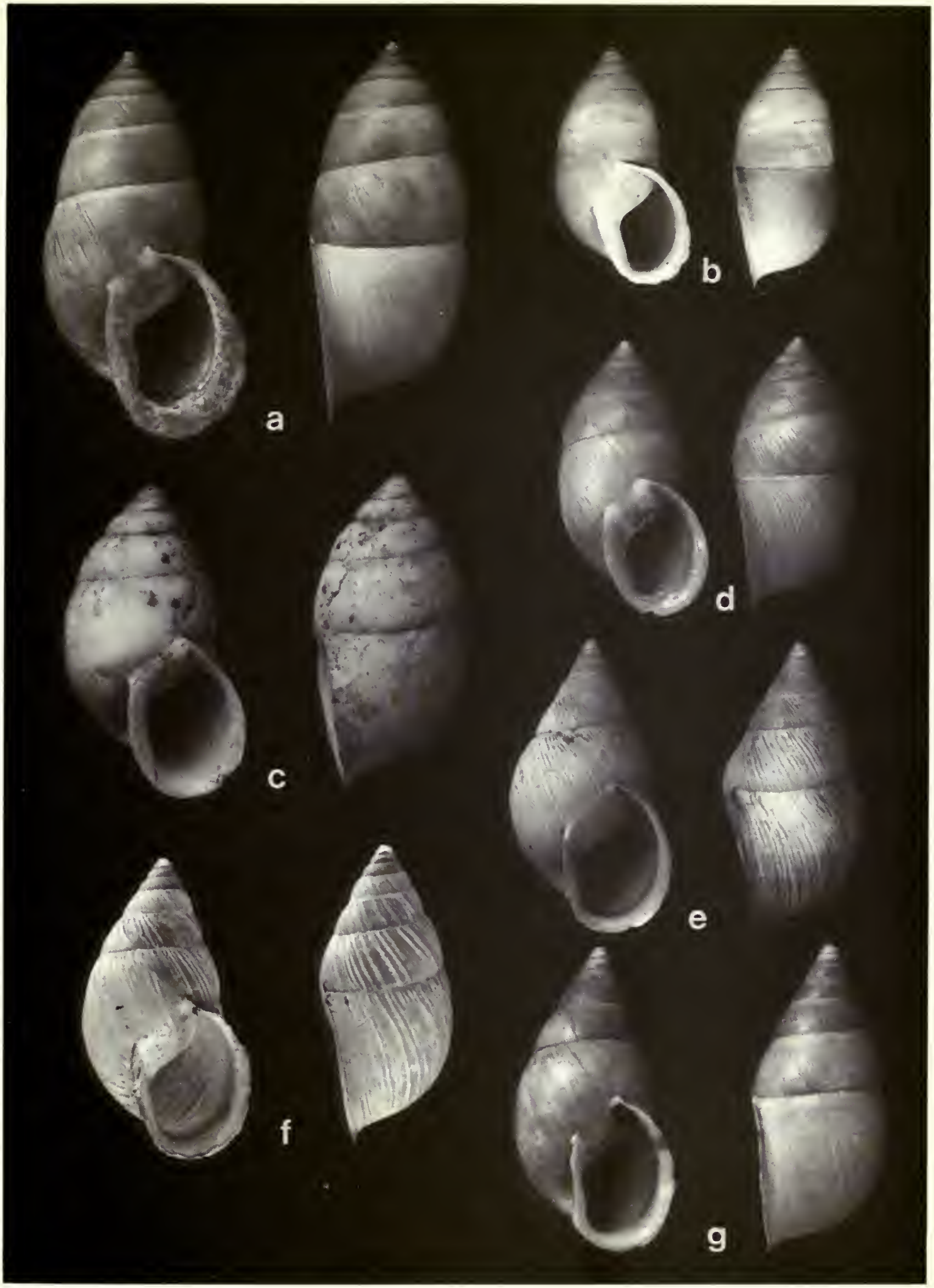
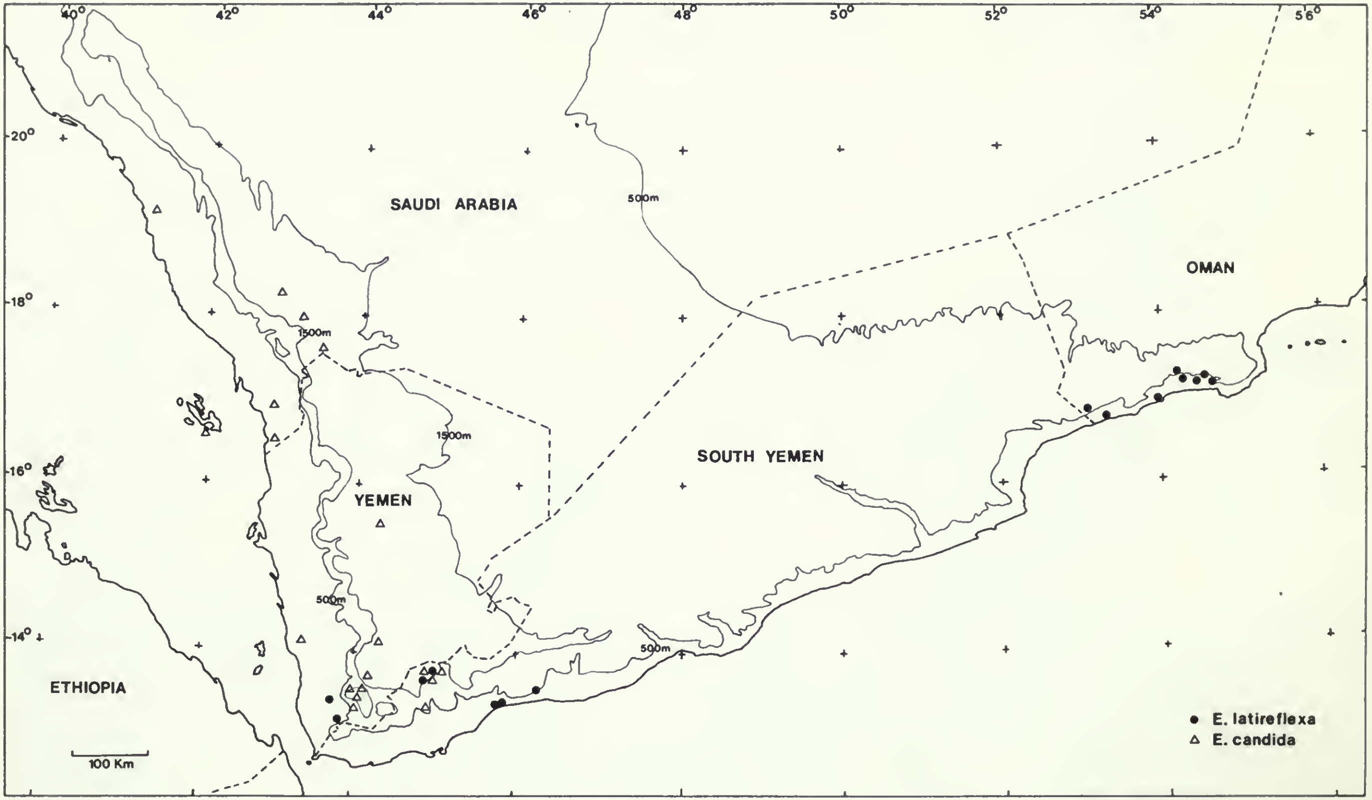


Fig. 16 *Euryptyxis candida:* a, Dhala, S. Yemen, BMNH 1939.4.19.26, × 1·5; b, Khamis Mishat, Saudi Arabia, BMNH 1945.8.23.187, × 1·5; c, Dumsuk Islands, Red Sea, BMNH 1928.3.16.33, × 3; d, possible type of *Pupa arabica* Forskal, ZMC, × 1·5; *Euryptyxis fragosa:* e. Hauban, RSM 1953.52.111, × 1·5; f, between Karia and al Seiyani, Yemen, MNHN, × 1·5; g, specimen ex Beck Collection, ZMC, × 1·5.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● E. latireflexa
△ E. candida

Fig. 17 Distribution map of *Euryptyxis candida* and *latireflexa*.

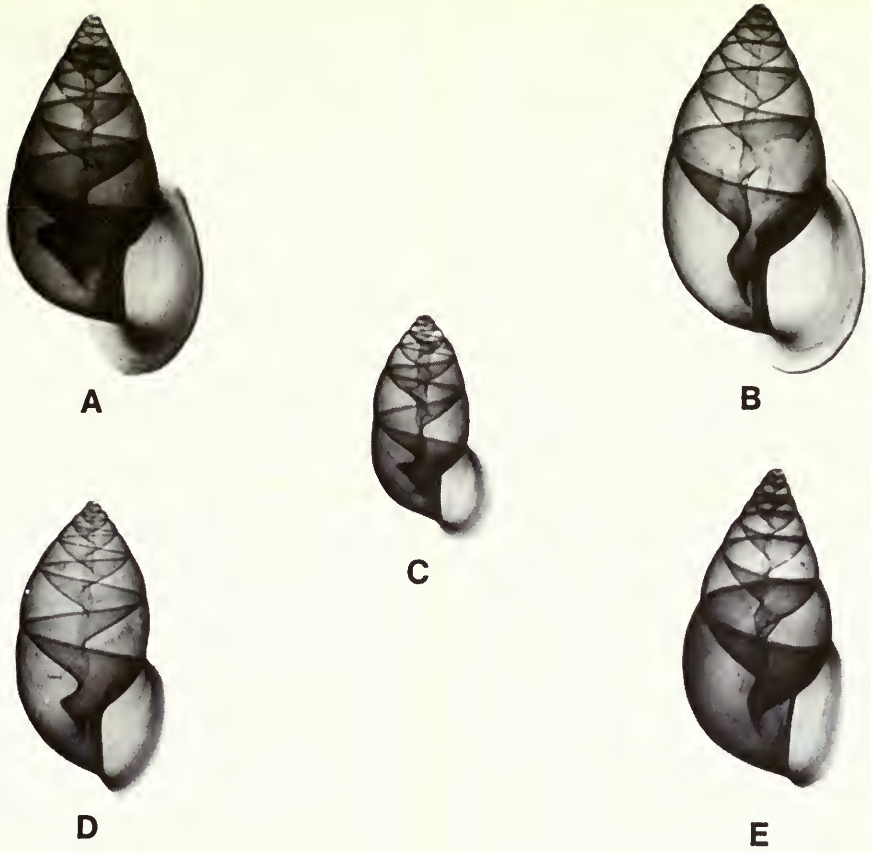

Fig. 18 X-ray photograph of *Euryptyxis* species to show relative development of the columellar fold; A, *latireflexa;* B, *revoili;* C, *labiosa;* D, *candida;* E, *fragosa;* × 1·4.

In fresh specimens the protoconch and early whorls are always a rich, glossy brown, typically becoming progressively paler until the shell becomes a milky transluscent grey/white. Occasionally the entire shell retains the brown colouration. In most specimens the internal lip surface has a brown rim, well illustrated by Delessert (1847, pl. 27, fig. 10).

Sculpture does not in general appear to vary greatly, with the sharp, regular radial striae always predominating. There is, however, a considerable range in size and, to a lesser extent, shape, although the latter is always characteristically pupiform. Material from coastal sites such as Jizan and Dumsuk Island are remarkable for their small size, and a more-elongate shape (the *forskali* form) appears to be characteristic of shells from the upland region of Asir in Saudi Arabia.

Body. Taizz specimens of a uniform cream colouration, with slightly darker pigmentation on tubercles of head.

Radula (Figs 19a–b). Total number of teeth per row in *candida* from Taizz between 40–42 (Table 2), although Hesse (1933) quoted a figure of 50 teeth for Menaha material. Central and lateral ectocones clearly developed but small. Mesocone of marginals rounded and ectocones bear single, wide pointed cusp; in some most marginal teeth ectocone becomes bicuspid.

Lung cavity. As in *E. latireflexa* (see below), with kidney extending 0·75–0·8 times cavity length. Outer lung wall weakly pigmented with brown and white streaks close to mantle collar.

Reproductive system. (Figs 20, 21). Hermaphrodite gland composed of 4 to 5 diffuse lobes, loosely imbedded in digestive gland and lying against parietal and columellar shell walls.

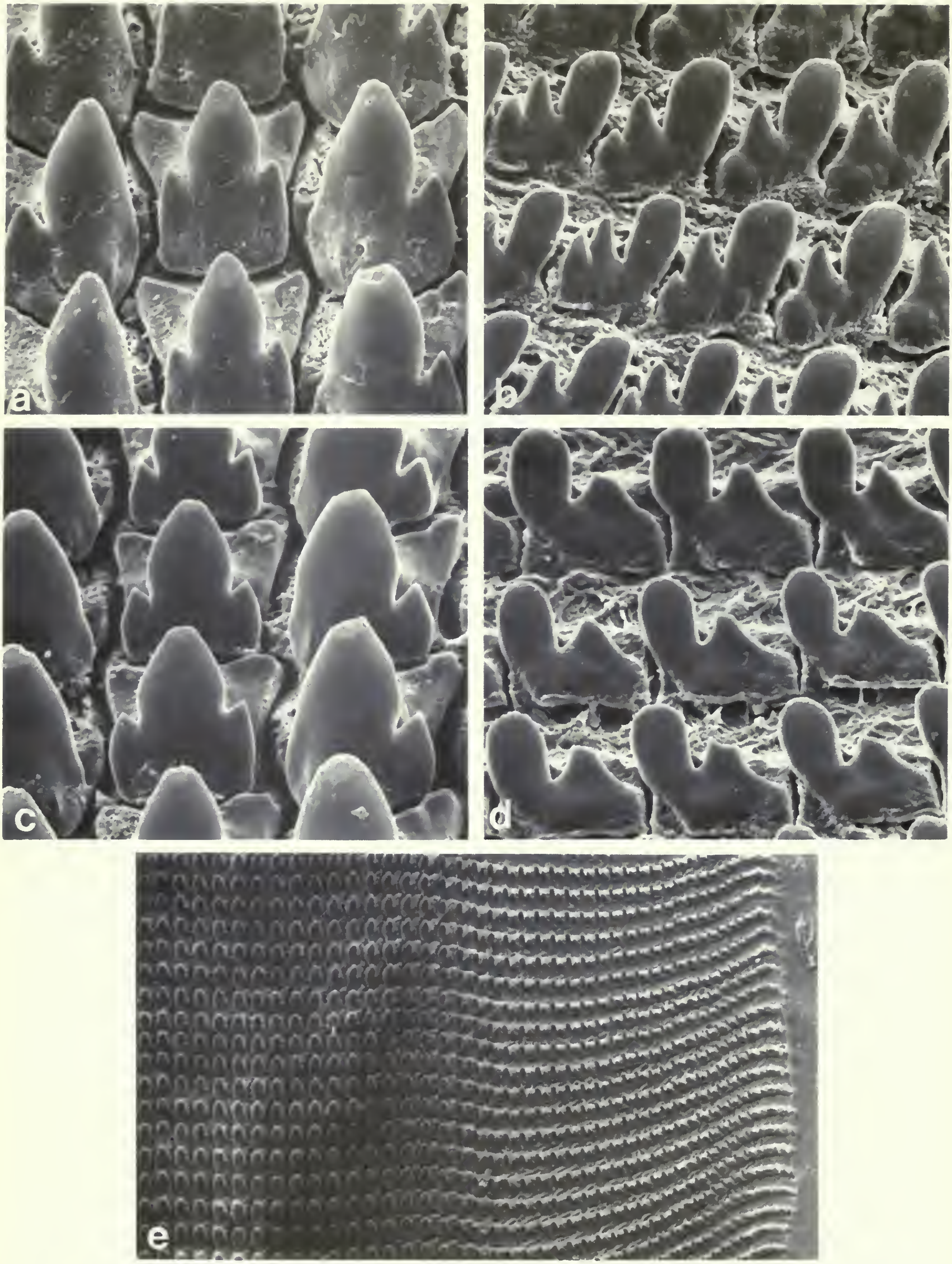

Fig. 19 Radular teeth of *Euryptyxis:* a, *E. candida,* Taizz, Yemen, 1979, central and lateral teeth; b, marginal teeth; c, *E. fragosa,* Taizz, Yemen, 1979, central and lateral teeth; d, marginal teeth; × 720; e, entire side of radula; × 80.

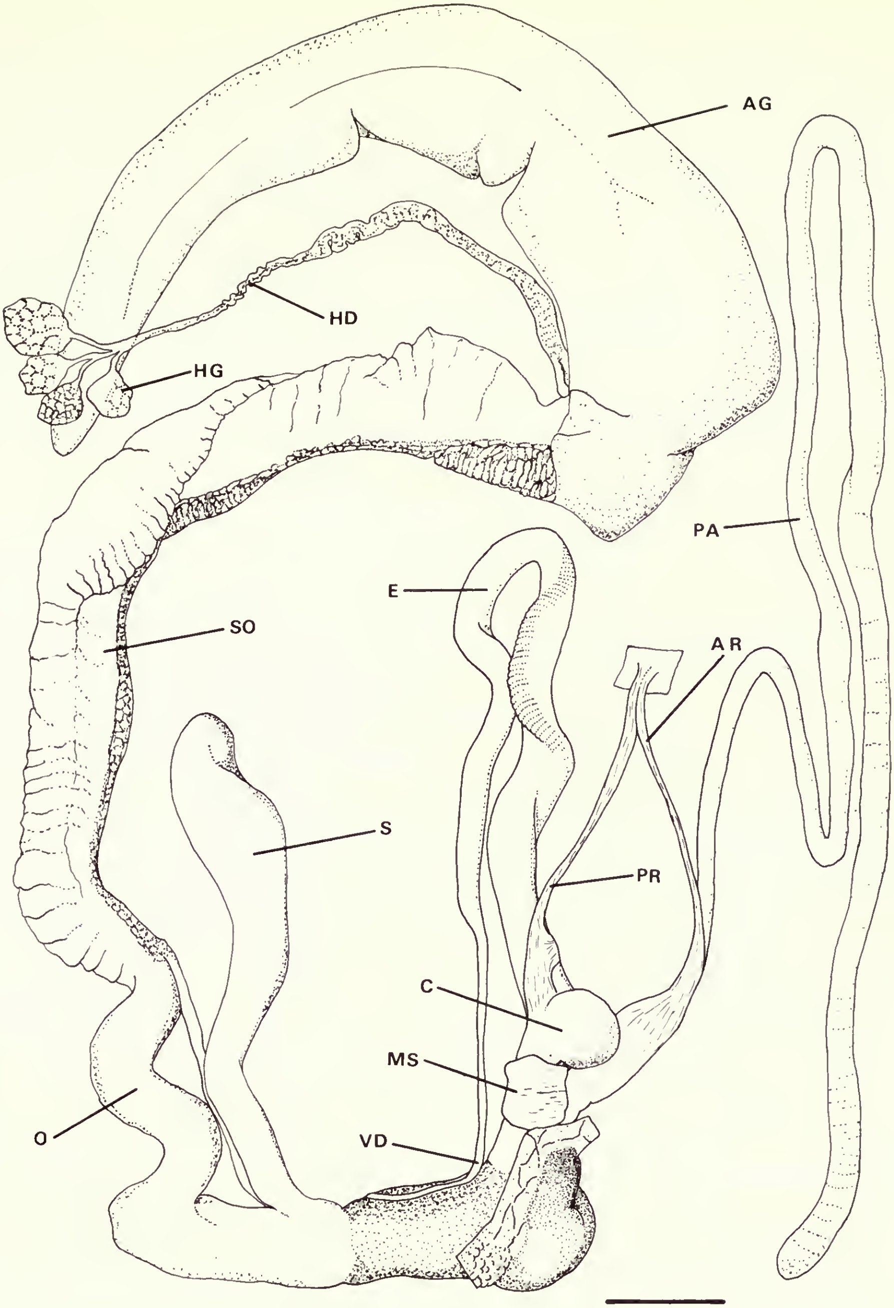

Fig. 20 Genital system of *Euryptyxis candida*, Taizz, 1979. Scale 2 mm.

Hermaphrodite duct long and thin, with elongate seminal vesicle (*sensu* Bayne, 1973) which is only weakly convoluted; talon simple fold in duct (Fig. 21B). Albumen gland relatively large for genus, 1·1–1·3 times length of spermoviduct.

Free oviduct about three times length of vagina, continuous with the atrium and darkly pigmented almost throughout its length; both attached to body wall by numerous short muscles.

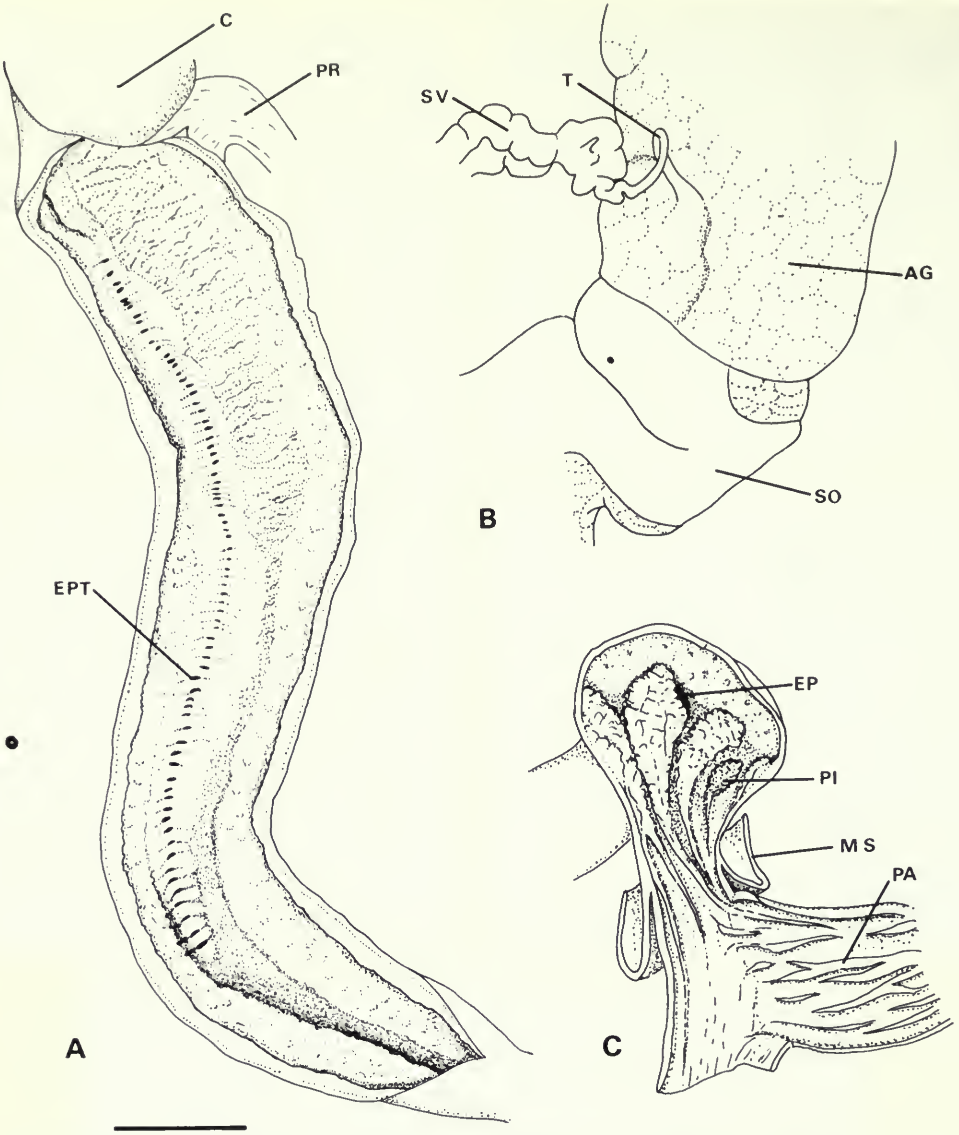

Fig. 21 *Euryptyxis candida,* Taizz, 1978: A, epiphallus; B, talon region; C, penis. Scale 1 mm.

Atrial retractor fairly strong, branching from main columellar muscle. Internally free oviduct bears weak, irregular longitudinal pillasters. Spermatheca approximately same length as free oviduct and not obviously separable into distinct head and stalk regions. Terminal portion of vas deferens differentiated into long epiphallus, about five times length of penis; externally with longitudinal row of transverse ridges, corresponding to line of internal pits, varying in number between 75 and 77 in the Taizz material (Fig. 21A). Epiphallus enters penis just below caecum.

Penis characterised externally by large, bulbous, thin-walled caecum at top; caecum may be globular or pointed. Penis small relative to other *Euryptyxis,* and has muscular collar or sheath, attached above and recurved at base to form two-layered structure (Fig. 21C). Internally are four principal glandular areas, three large and one very much smaller, which continue downwards as tapering pilasters. Pattern asymetrical: two large glandular patches, which appear almost fused, lie to one side of epiphallar pore, with remaining large and small areas quite distinct on other side, overlying point of entry of the appendix at base of penis. Appendix clearly divisible into three distinct regions: a short, wide basal portion, internally lined with reticulum of predominantly longitudinal pilasters; a long, thin, thick-walled central portion with a narrow lumen; and a wider, terminal saculate portion of similar length but with very thin, transparent wall. Penis and appendicular retractor muscles originate together about one third way up lower lung wall; may initially be fused over a short distance. Penis retractor bifurcates prior to insertion, one branch inserting transversely at penis/epiphallus junction, other laterally just above, on epiphallus proper.

COMMENTS. Although *candida* exhibits enormous variation in size, the shape and sculpture of the shell are relatively constant, and it is significant that all smaller specimens are from coastal locations. Its pupiform shell shape and strong, regular radial ribbing combined with aflared but unreflexed lip distinguish it from other *Euryptyxis*.

Reproductive anatomy is most similar to *E. fragosa,* but at Taizz, Yemen where both are sympatric, there are differences in the epiphallus and penial appendix.

Euryptyxis fragosa (Pfeiffer, 1842)

Bulimus fragosa Férussac, 1821–2:59. [Les Grandes Indes], *nomen nudum.*
Buliminus fragrosus Férussac. Beck, 1837:68. *nomen nudum.*
Bulimus fragosus Férussac. Pfeiffer, 1842:45. [Yemen].
Bulimus fragosus Férussac. Küster & Pfeiffer, 1845–55:62, pl. 18, figs 1, 2; Bourguignat, 1882:14, fig. 19.
Buliminus fragosus Férussac. Rossmässler, 1880:41, pl. 198, fig. 1983.
Buliminus fragosus Pfeiffer. Westerlund, 1887:64.
Buliminus (Petraeus) fragosus Férussac. Kobelt, 1902:406, pl. 172, fig. 1.
Euryptyxis fragosa Pfeiffer. Connolly, 1941:30.
Euryptyxis fragosus Pfeiffer. Fisher-Piette & Métivier, 1972:1293.

TYPE MATERIAL. Férussac's original naming of this species was invalid, the first comprehensive description being given by Pfeiffer (1842). However, Pfeiffer's original material has not been traced and may possibly have been lost with the destruction of the Dohrn Collection in the Stettin Museum during the 1839–45 war (Dance, 1966:285). Two shells labelled *Helix fragosa* Fér. were found in the Férussac collection in Paris but these are *E. candida.*

OTHER MATERIAL. **Yemen:** El Kubar, leg. G. W. Berry, BMNH 1908.2.21.3, (1 spec.); Wadi Dhulla, 5 miles NW. Sana, c. 2500 m., leg. P. W. R. Petrie, vii.1938, BMNH, (26 specs.); Taizz district, 1250–1550 m., BMNH 1939.4.19.18, (1 spec.); Hauban, nr. Taizz, leg. A. R. Waterson, 7.viii.1946, RSM 1953.52.111, (7 specs.); 30 miles S. Taizz, 1250 m. leg. A. R. Waterson, 13.xii.1945, RSM 1953.52.114, (5 specs.); near Taizz, leg. A. R. Waterson, 8.iii.1946, BMHN 1948.9.7.4–13, (10 specs., 3 dissected); near Taizz, 1250 m., leg. A. R. Waterson, 13.xii.1946, RSM 1953.52.102, (3 specs,); Between Rahida and Taizz, leg. A. R. Waterson, 7.xii.1945, RSM 1953.52.113, (22 specs); 5 miles from Taizz, leg. M. R. Brunt and J. D. Mather, xi.1973, BMNH, (3 specs.); Al Seiyani, 32 km. N. Taizz, leg. M. Lavranos, 1977, MNHN, (2 specs.); Wadi Shadbh, 35 km W. Menakha, 1400 m, leg J. Lavranos, 1977, MNHN (2 specs); Al Maghriba, 5 km W. Menakha, leg. J Lavranos, 1977, MNHN (5 specs); Between Karia and Al Seiyani, 1600 m., leg. M. Lavranos, 1979, MNHN, (8 specs.); Hamman Ali, leg. M. Lavranos, 1978, MNHN, (5 specs.); Qubesh, 1700 m., leg. M. Lavranos, 1979, MNHN, (2 specs.); Taizz, 1400 m, leg. P. Heath, iv. 1978, BMNH 1982, (2 specs., 2 dissected); Al Hyma, near Taizz, 1100 m., leg. P. Heath, ix.1979, BMNH 1982, (4 specs., 3 dissected); **South Yemen:** Wadi Leje, Jebel Jihaf, leg. H. Scott, BMNH 1939.4.19.1–8, (7 specs.); Jebel Jihaf, 1200 m., leg. H. Scott, BMNH 1939.4.19.21–24, (4 specs., 2 dissected); Jebel Jihaf, 1950–2050 m., Leg. H. Scott, BMNH 1939.4.19.25, (1 registered spec., 14 further unregistered specs.); Dhala, 1500 m., leg. H. Scott, 12–14.ix.1937, BMNH, (4 specs.); Mukieras, leg. G. Lancaster Harding, 1958, (11 specs).

DISTRIBUTION (Fig. 22). The most restricted of the four recognised Arabian *Euryptyxis* species. Almost all of the material examined here was collected in and around Taizz, although conchologically similar material has been recorded as far north as Manakha. The relatively smooth, slender form was found abundantly at Jebel Jihaf, near Dahla in in South Yemen, but also near Hamman Ali, between Yarim and Sana'a.

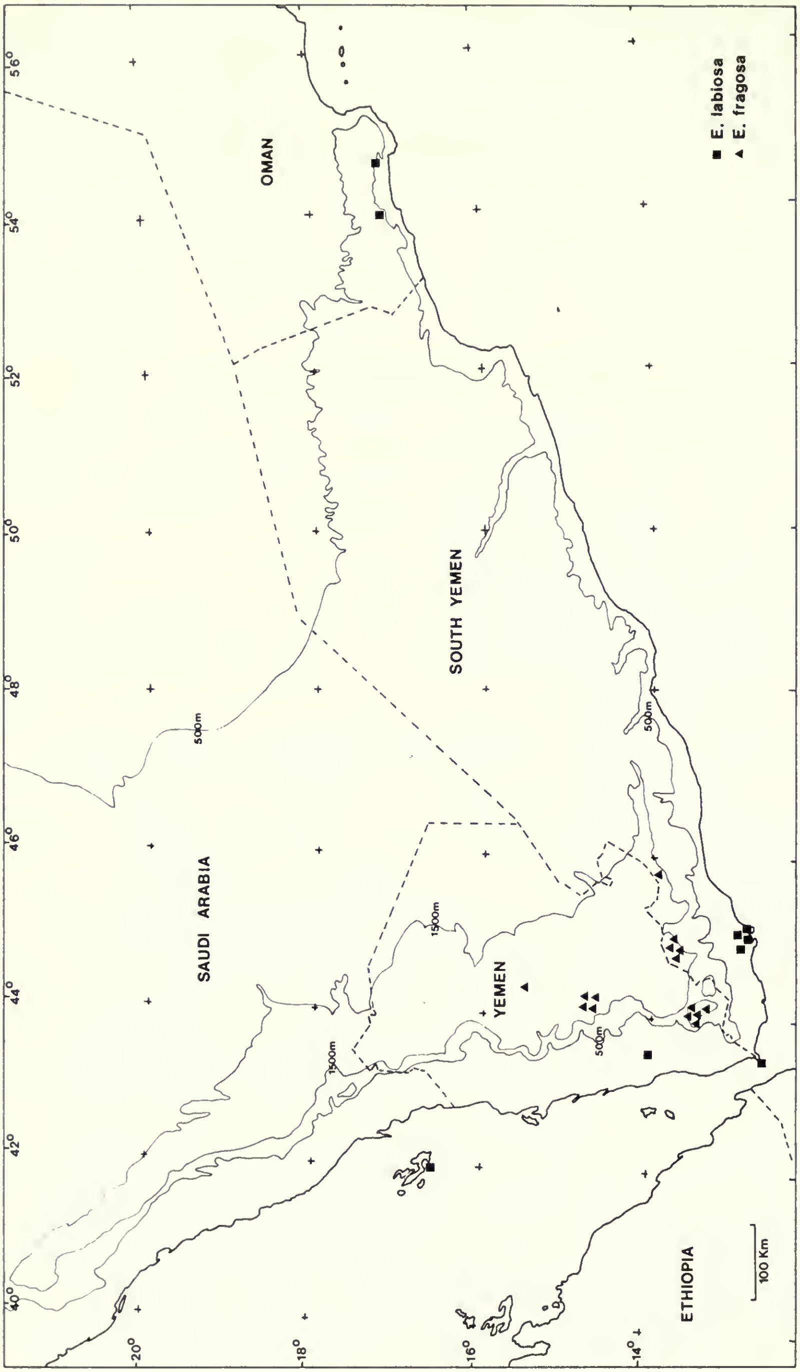
SAUDI ARABIA
OMAN
SOUTH YEMEN
YEMEN
ETHIOPIA
500m
500m
500m
1500m
1500m
40°
42°
44°
46°
48°
50°
52°
54°
56°
20°
18°
16°
14°
■ E. labiosa
▲ E. fragosa
100 Km

Fig. 22 Distribution map of *Euryptyxis labiosa* and *fragosa*.

Description. Dextral, *rounded elongate conical;* surface with regular radial ribbing varying from coarse to very fine, *becoming less evenly spaced, wavy, and usually weaker towards the aperture,* and fine wavy spiral striae; protoconch smooth, becoming ribbed; umbilicus closed. Aperture with *flared lip, never recurved; no internal columellar tooth* (Fig. 18E). Colour opaque white, rarely greyish brown with white ribs.

Shell. Dimensions: Taizz, Yemen, leg. Waterson, 1946: 30·0 × 15·1 × 13·3; 14·2 × 10·0; lip 1·6; 8·7 wh. Taizz, Yemen, leg. Heath, 1979: 35·8 × 19·1 × 16·6; 19·1 × 13·7; lip 2·9; 8·6 wh. Jebel Jihaf, South Yemen, leg. Scott: 28·8 × 15·0 × 12·7; 14·5 × 10·0; lip 1·3, 8·2 wh.

The principal sculptural variation is found in the radial ribbing which may be very strong (Fig. 16F), as in some populations around Taizz, or almost absent (Jebel Jihaf); other populations in the Taizz region have intermediate sculpture. Coarse ribbing appears in general to be correlated with a rather wider shell than normal, whereas the smoother shells are more slender in profile; individual populations show little variation in either respect.

Body. Uniformly pale cream, with slight dark pigmentation on tubercles in head region.

Radula (Figs. 19c–e). Very similar to *E. candida* (see Table 2).

Lung cavity. Typical for genus (see *E. latireflexa* below), but kidney relatively shorter than other species, occupying 0·7 times lung length (Table 3). Outer wall of lung unpigmented.

Reproductive system (Figs 23, 24). Albumen gland relatively short and narrow, approximately 1/3 length of spermoviduct. Spermatheca about 1·5 times as long as free oviduct; in one specimen it contained fragments of a partly dissolved spermatophore: tail region complete and shaped much as in *Zebrinops*; one complete digitiform spine also present (Figs. 24C–D).

Epiphallus thick, externally bears strong transverse ridges corresponding internally to longitudinal row of 40 to 57 pits (Figs. 24A). Penis with globular caecum (smaller than in *E. candida*) and sharply recurved muscular sheath. Penis and appendicular retractor muscles originating separately but at same leve on lung wall; former has multiple insertion on epiphallus, and main branch to penis. Internally, penis with rather variable pilaster pattern. Within individual Taizz populations, overall distribution of glandular patches and pilasters similar, but differences present in degree to which the two lateral glandular areas embraced epiphallar pore, and also in separation of these from their downward extensions by the transverse groove. Also differences in number, strength and regularity of pilasters in base of penial appendix.

Penial appendix characterised by thickening of basal region of central stalk (Fig. 23), unlike other Arabian *Euryptyxis*; thickening more marked in Taizz specimens than in those from Jebel Jihaf, but clearly developed in latter. Insertion of appendicular retractor muscle normal for genus.

Comments. Despite considerable inter-population variation in shell sculpture and shape, specimens from three populations from Taizz showed a close degree of similarity in their anatomy. The sample from Jebel Jihaf, whilst being much smoother and more slender than any of the Taizz examples, was anatomically similar, and the number of epiphallar pits (48–49) was within the range shown by the Taizz material (40–57) (Table 5).

The species is characterised both by the number of epiphallar pits and the enlarged base of the central part of the penial appendix. All the forms agree in having a generally conical outline to the shell (as opposed to the pupiform shape of *candida*), a lip which is flared but never reflexed, a very weakly developed columellar fold, and distinct, regular spiral striae. These conchological similarities, in conjunction with the overall anatomical similarities, suggest that in the present state of knowledge all the forms should be included within a single species.

Eurypyxis labiosa (Müller, 1774)

Helix labiosa Müller, 1774:96. [In India].
Helix arabica Forskal, 1775:127. [Loharjae].
Helix cylindracea acuta Martini & Chemnitz, 1786:166, pl. 135, fig. 1234. [*nomen nudum*].
Helix labiosa Müller. Gmelin, 1791:3645; Dillwyn, 1817:347.
Bulimus labiosus Bruguière, 1792:347.
Buliminus labiosa Müller. Beck, 1837:69.

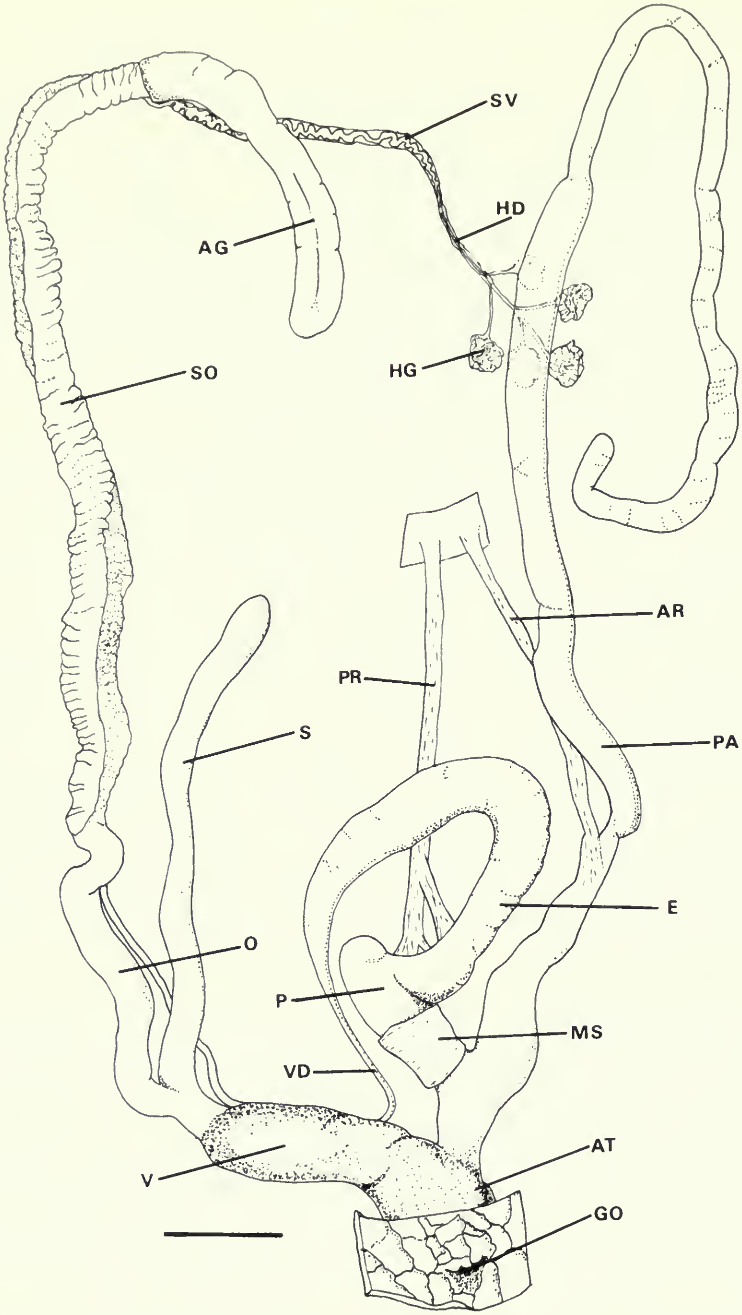

Fig. 23 Genital system of *Euryptyxis fragosa,* Taizz, Yemen, 1979. Scale 2 mm.

Pupa jehennei Récluz, 1843*a*:4; 1843*b*:pl. 76. [Socotra].
Bulimus labiosus Müller. Küster & Pfeiffer, 1845–55:48, pl. 15, figs 1, 2; Pfeiffer, 1848:67; Reeve, 1849: pl. LX, species 412; Bourguignat, 1882:20, fig. 11.
?*Bulimus bruguieri* Bourguignat, 1882:25. [? loc.].
Buliminus labiosus Müller. von Martens, 1889:149.
Buliminus (Petraeus) labiosus Müller. Rossmässler, 1893:84, pl. 171, fig. 1107.

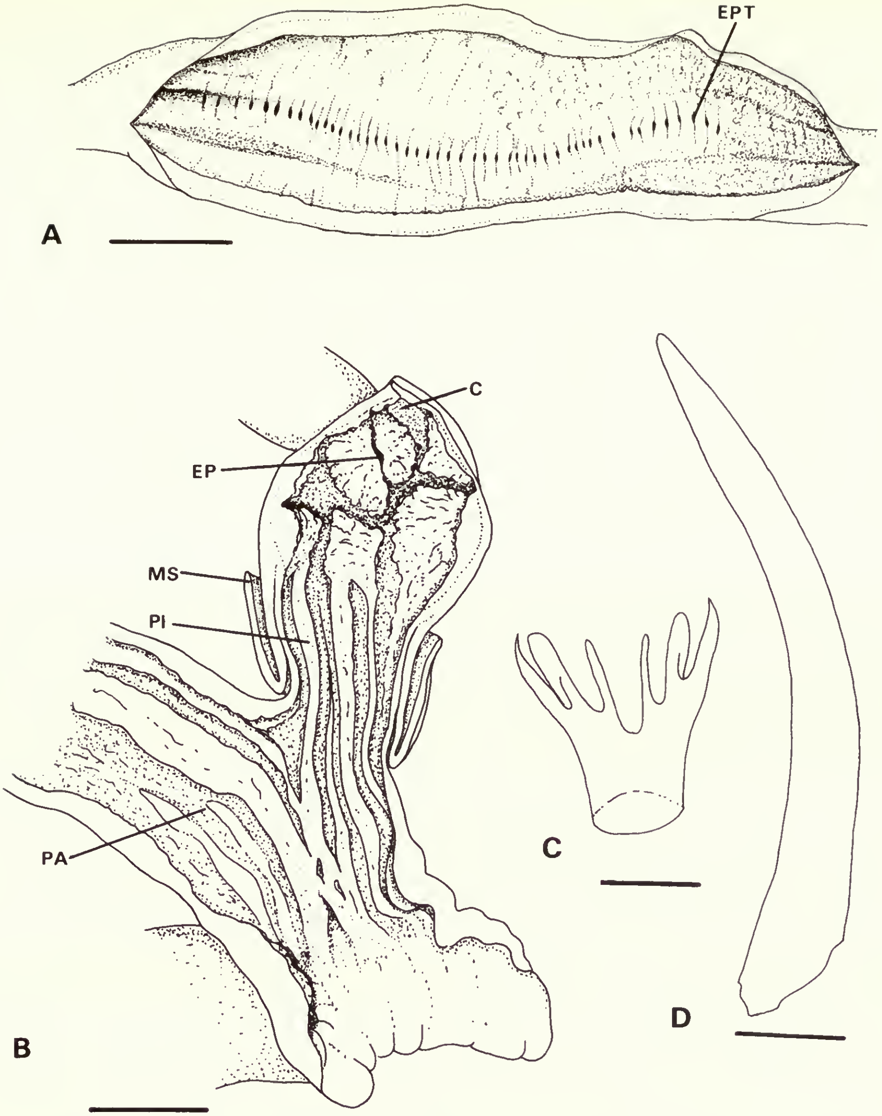

Fig. 24 *Euryptyxis fragosa,* Taizz, Yemen, 1979: A, epiphallus, scale 1 mm; B, penis, scale 1 mm; C, spermatophore spine, scale 0·2 mm; D, spermatophore tip, scale 0·5 mm.

Bulimulus hypodon Pilsbry, 1897:102. [Lower California].
Euryptyxis labiosus jehennei Petit. Pilsbry, 1897–8:156, p121, figs 5–7
Buliminus (Petraeocerastus) labiosus Müller, Kobelt, 1902:890, pl. 127, figs 6–9.
Euryptyxis labiosa Müller. Mordan, 1980*a*:360, fig. 2k; 1980*b*:106, pl. 2.

TYPE MATERIAL. Possible Syntype of *jehennei* Récluz, Petit Collection, BMNH 1843.11.27.88. Holotype of *hypodon* Pilsbry, California *sic,* ANS.

The material described by Müller in his *Vermium terrestrium et fluviatilum* . . . of 1774 is housed in the Zoological Museum, Copenhagen but I have been unable to trace the types of *labiosa* there. Although the original description of *labiosa* is arguably ambiguous in the absence of types, the subsequent usage of the Müller's name is clear and his authorship is retained. Pilsbry's naming of *hypodon* clearly arose from an erroneous locality.

Table 5 Numbers of pits in the epiphallus of *Euryptyxis* species

Species	Locality	no. specs.	no. pits.
E. candida	Taizz, Yemen, 1978	2	76–77
	Taizz, Yemen, 1979 £	2	75–77
E. latireflexa	Dahaq Thu'ari, Dhofar, 1940	2	19–20
	Khadrafi, Dhofar, 1976	3	17–23
	Ain Arzat, Dhofar, 1976	10	17–26
	Tawai Atair, Dhofar, 1978 $	2	19–28
	Salalah, Dhofar, 1981	1	24
E. fragosa	Taizz, Yemen, 1946	3	40–42
	Jebel Jihaf, S. Yemen, 1938	2	48–49
	Taizz, Yemen, 1979 £	2	52–53
E. labiosa	Tawai Atair, Dhofar, 1981 $	2	30–32
E. revoili	Nogal, Somalia, 1961	2	24–25

£, $ Syntopic species pairs.

Other material. **Yemen:** Menaka, leg. Schweinfurth, BMNH 1895.8.20.3, (1 spec.); Senna [? = Sana, Wadi Hadramaut, c 500 m], leg. Preston, 5.x.1903, BMNH, (3 specs); Senna, RSM 1961.61, Salisbury Colln., (1 spec.); 6 miles W. of Heis, leg. A. R. Waterson, 13.xii.1945, RSM 1953.52.117, (6 specs). **South Yemen:** Aden, leg. A. E. Craven, vii.1877, BMNH 1880.10.1–2, (2 specs.); leg. A. W. Baynham, BMNH 1885.8.9.12–14, (3 specs); leg. Yerbury, BMNH 1888.4.9.354, (1 spec.); leg. Shopland, BMNH 1902.5.14.1–5, (5 specs.); leg. W. Blume, BMNH 1937.12.30.2215, (1 spec); leg. Shopland, 1937.12.30.2216–17, (2 specs.); leg. Lander, BMNH, (13 specs); Gold Mohur Valley, Aden, leg. A. J. Piele, RSM 1961.61, (7 specs.); Perim Island, leg. J. J. Walker, BMNH 1891.1.31.189–91, (3 specs, and 2 unregistered). **Saudi Arabia:** Dumsuk Island, Farsan Islands, leg. W. Macfadyen, BMNH 1928.3.16.29–32, (4 specs.); BMNH 1937.12.30.2225–32, (8 specs); Habile, leg. J. Lavranos, 1980, BMNH (5 specs); **Oman:** Dhofar, Leg. Mrs J. T. Bent, 1894–5, BMNH 1898.12.4.21–3, (3 specs.); Tawi Atair, Jabal Samhan, leg. M. D. Gallagher, 9.iv.1977, BMNH, (5 specs.); leg. M. D. Gallagher, 30.iv.1978, (17 specs., 3 spirit, 2 dissected); leg. J. N. Barnes, 15.iii.1980, BMNH, (6 specs.); between Ayub and Teetam, Jabal Qara, 800 m., leg. M. D. Gallagher, 31.viii.1982, BMNH, (3 specs.).

Distribution (Fig. 22). It is difficult to assess the precise range of this species, which could occur almost continuously from Dhofar to the south-eastern coast of the Red Sea, although almost all the material considered here is either from localities in Dhofar, or the environs of Aden where the snail seems to be particularly abundant. Odd specimens from the Hadramaut [Preston], and the Tihama of Yemen [Waterson] and Saudi Arabia [Lavranos] do, however, suggest such continuity. In addition to the continental distribution, *labiosa* has been recorded from the Farsan and Perim Islands in the Red Sea, as well as Socotra (the type locality of *jehennei*), Cape Gardafui, Somalia (Bourguignat, 1882:31), and one doubtful record from the Seychelles. All records are from sites at comparatively low elevations, the highest being 800 m in Dhofar.

Description. Dextral, *elongate pupiform,* surface with regular radial ribs becoming weaker and more widely spaced towards aperture, and fine wavy spiral striae; protoconch smooth becoming strongly ribbed; umbilicus closed. Aperture with *recurved lip, and strong internal columellar tooth* (Fig. 18C). Colour usually transparent or opaque white, may be tinged with brown; lip white.

Shell. Dimensions of syntype *jehenni* Récluz: 25·1 × 12·0 × 9·2; 12·1 × 9·3; lip 2·5; 8 wh. Holotype of *hypodon* Pilsbry (Fig. 25e): 25 × 12·5; 13·0 × 10·2; lip 2·3; 7·5 wh. Largest specimen, Aden, leg. Baynham: 23·9 × 11·5 × 9·3; 11·5 × 9·1; lip 2·2; 7·3 wh. Tawai Atair, Dhofar. leg. Gallahagher: largest: 21·4 × 10·8 × 9·3; 9·9 × 8·7; lip 1·5; 7·2 wh. Smallest: 15·9 × 8·9 × 8·1; 7·8 × 6·0; lip 1·0; 6·2 wh.

Shell shape varies considerably within the species, even within samples from a single site. This is exemplified by the results of a statistical comparison of three 'age classes' of shells: living,

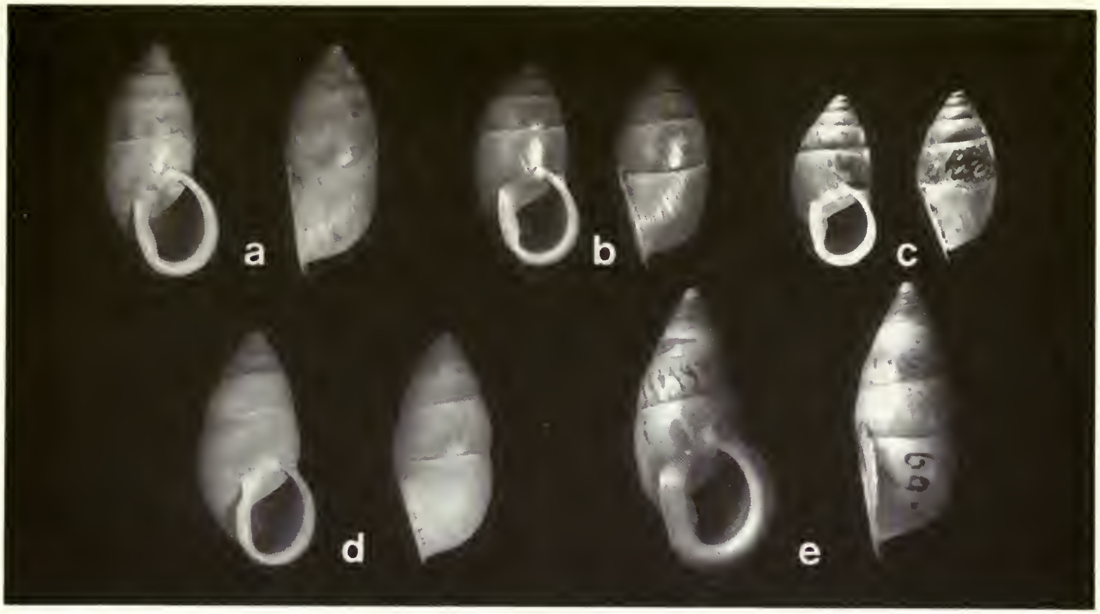

Fig. 25 *Euryptyxis labiosa:* a-c, Tawai Atair, Oman, BMNH; d, Dumsuk Island, Read Sea, BMNH 1928.3.16.29; e, holotype of *Bulimulus hypodon* Pilsbry, ANS 23029. All × 1·5.

recently dead (intact periostracum), and long dead (periostracum lost) collected at Tawai Atair in 1978, (Table 6). Despite small sample size, there were highly significant differences between the long-dead category and each of the other two categories for almost all shell parameters, whilst there were few significant differences between the latter pair. There also appear to be geographical differences, at least for some shell characters. Whereas shells from Aden seem to show a similar degree of shape variation to those from Dhofar, the former are typically more elongate and tend to have a wider lip (*c.* 2 mm. compared with 1–1·5 mm. for Dhofar).

Body. Darkly pigmented, becoming almost black towards head region.

Lung cavity. Similar to other *Euryptyxis* species, with kidney extending 0·75–0·8 times length of lung (Table 3). Outer lung wall strongly pigmented with black and opaque white irregularly shaped patches, clearly visible through shell (Mordan, 1980b: pl.2).

Radula (Figs 26a–b). Overall size of radula markedly smaller than in other *Euryptyxis,* but individual tooth size not greatly different; total number of teeth per row lower because fewer marginals (Table 2).

Reproductive system (Fig. 27). Albumen gland about half length of spermoviduct, and spermatheca only slightly longer than free oviduct. Relative length of vagina/atrium complex as in other *Euryptyxis* but much wider, being more than twice width of free oviduct. Details of terminal male system similar to *E. latireflexa,* although overall dimensions much smaller.

Differences as follows: number of pits in epiphallus greater, being 30–31 (Table 5; Fig. 27c); appendix enters higher up penis; appendicular retractor does not ensheath mid-portion of appendix prior to insertion. Arrangement of pillasters within penis similar to *E. latireflexa,* but a well-defined transverse groove just below epiphallar pore separates pair of lateral pillasters surrounding pore from their downward extensions (Fig. 27B); pilaster pattern within base of appendix as in *E. latireflexa.*

COMMENTS. In both shell and soft anatomy this species most closely resembles *latireflexa,* with which it co-occurs in Dhofar, but at Tawai Atair there are differences in penial and epiphallar anatomy, and the adult shell is distinctly smaller throughout its range.

Table 6 Comparison of shell dimensions in living, recently dead, and long-dead shells of *Euryptyxis labiosa* from Tawai Atair, Dhofar, Oman, 30.iv.1978. Student's t Test (unequal variance).

Parameter	Living (n=3)		Rec. dead (n=8)		Long-dead (n=6)		Living/ long-dead		Living/ rec. dead		Rec. dead/ long-dead	
	x	s.d.	x	s.d.	x	s.d.	t	d.f.	t	d.f.	t	d.f.
Shell ht.	17·03	0·84	16·92	0·84	20·62	5·7	8·11	5 ***	0·23	7 ns	9·81	14 ***
Shell max. diam.	9·23	0·31	9·24	0·26	10·68	5·2	5·26	9 ***	0·2	4 ns	6·25	8 ***
Shell min. diam.	7·6	0·27	7·94	0·31	9·0	5·1	5·39	9 ***	1·8	6 ns	4·5	9 **
Apert. ht.	8·63	0·21	8·62	0·45	9·81	4·5	5·62	9 ***	0·4	11 ns	5·1	13 ***
Apert. diam.	6·47	0·25	6·48	0·24	7·5	2·3	5·92	5 **	0·12	5 ns	7·8	13 ***
Lip width	1·17	0·12	1·15	0·11	1·28	0·18	1·16	9 ns	0·22	5 ns	1·58	8 ns
No. whorls	6·06	0·25	6·38	0·13	6·59	0·39	4·17	6 **	1·92	3 ns	4·75	8 ns
Spire Index	2·24	0·03	2·13	0·13	2·3	0·13	1·01	9 ns	2·25	9 ns	2·39	13 *

***p<0·001
**p<0·01
*p<0·05
ns not significant

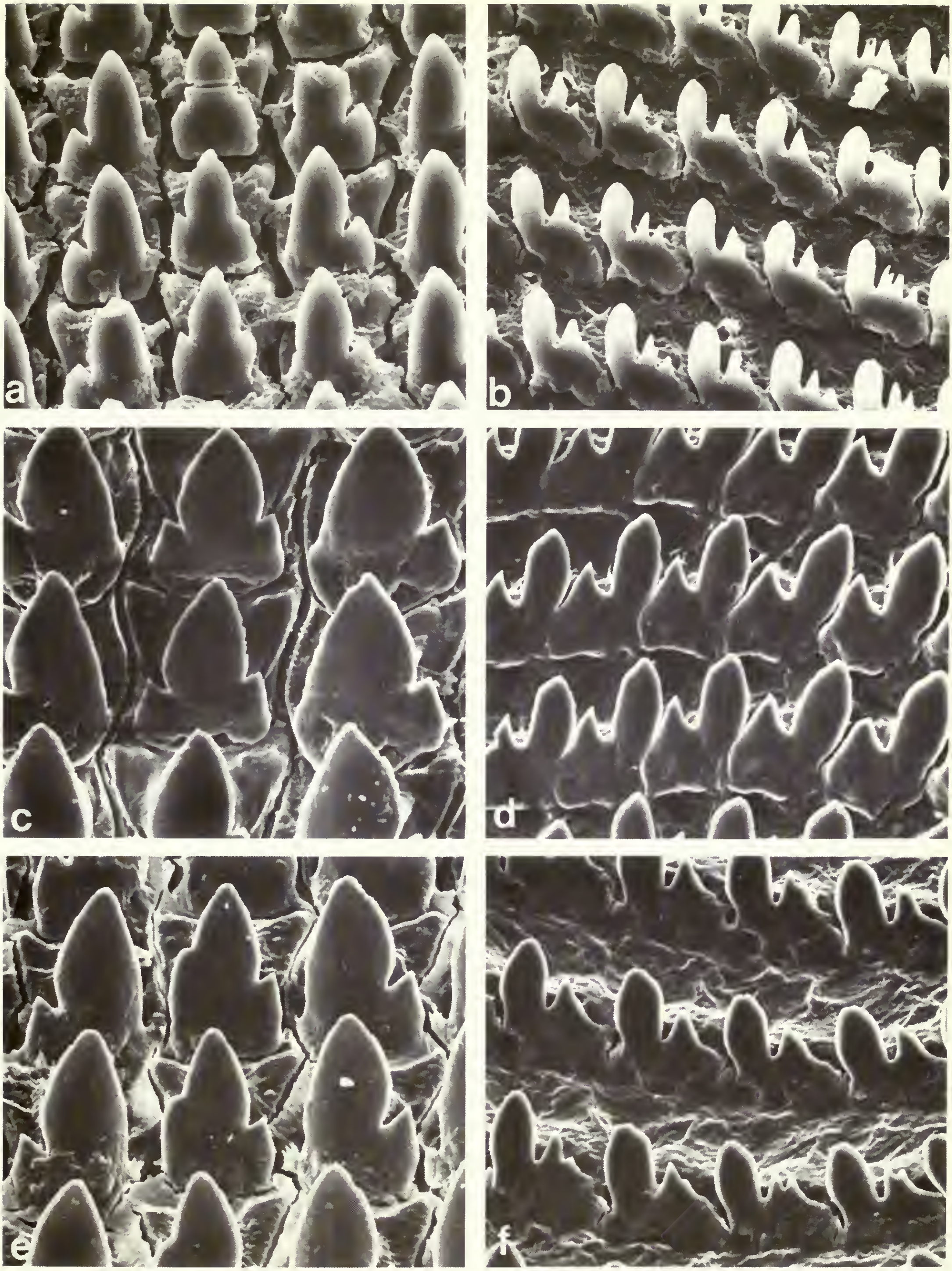

Fig. 26 Radular teeth of *Euryptyxis:* a, *E. labiosa,* Tawai Atair, Oman, 30.iv.1978, central and lateral teeth; b, marginal teeth; c, *E. latireflexa,* Tawi Atair, Oman, 30.iv.1978, central and lateral teeth; d, marginal teeth. e, *E. latireflexa,* Ain Arzat, 31.v.1976, central and lateral teeth; f, marginal teeth; × 720.

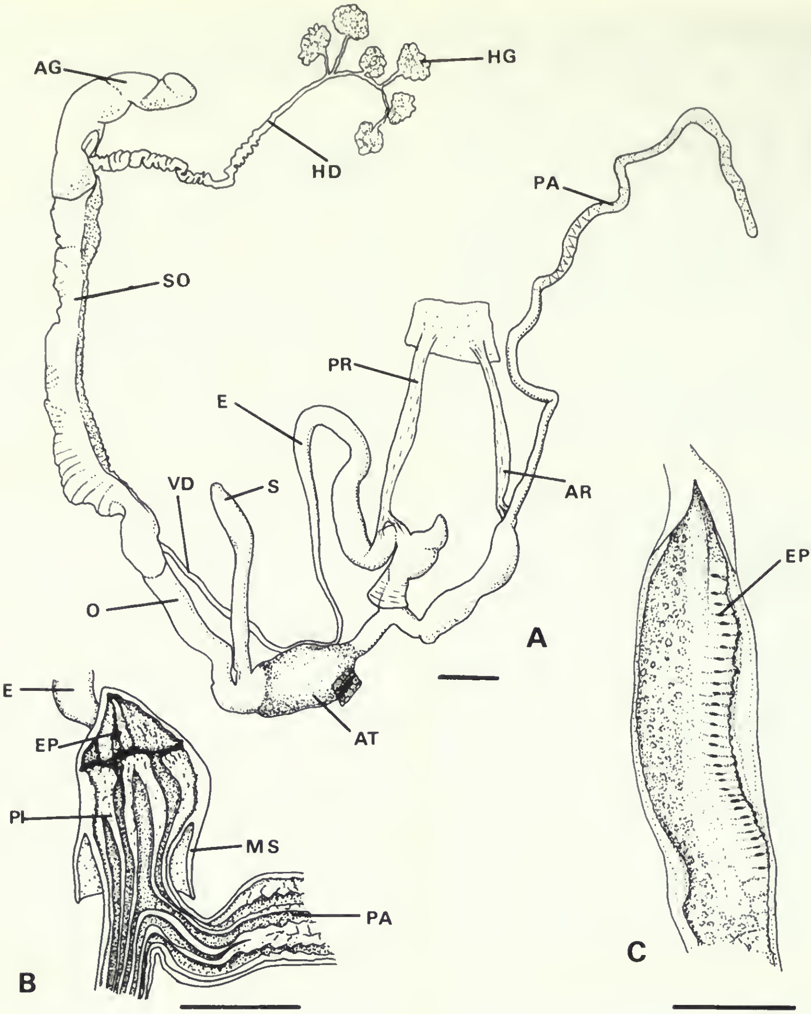

Fig. 27 *Euryptyxis labiosa,* Tawi Atair, Oman, 1978: A, Genital system; B, Penis; C, Epiphallus. Scale 1 mm.

Euryptyxis latireflexa (Reeve, 1849)

Bulimus latireflexus Reeve, 1849, pl. LXXVII, species 568. [Muscat?].
Bulimus latireflexus Reeve. Bourguignat, 1882:19, fig. 22.
Bulimus micraulaxus Bourguignat, 1882:17, fig. 20. [sud de Arabie].
Bulimus micraulaxus Bourguignat. Westerlund, 1887:62.
Buliminus lunti Melvill, 1894:224, pl. XIV, fig. 7. [Plateau 400 miles east of Aden, Hadramaut]. Melvill & Ponsonby, 1896:1.
Buliminus (Petraeus) lunti Melvil. Rossmässler, 1896:96, pl. 207, fig. 1305.
Bulimus deflersi Jousseaume, 1894:100. [Gebel el Areys].
Petraeus socialis Jousseaume, 1899:8. [Schoukra].
Petraeus schoukraensis Jousseaume, 1899:8. [Schoukra].
Buliminus (Petraeocerastus) schoukraensis Jousseaume. Kobelt, 1902:989.
Bulimus (Petraeomastus) socialis Jousseaume. Kobelt, 1902:991.
Cerastus dinshawi Sykes, 1902:338. [Senna].
Buliminus (Petraeocerastus) dinshawi Sykes. Rossmässler, 1906:58, pl. 329, fig. 2061.

Euryptyxis lunti var. *makallensis* Pallary, 1925:224, pl. XXXV, fig. 22. [Makalla; Gebel el Da'liya].
Euryptyxis littlei Pallary, 1925:224, pl. XXXV, fig. 21. [Gebel el Da'liya; Gebel Mihta; Qarn el Ghail].
Euryptyxis littlei var. *minor* Pallary, 1925:224. [as above].
Euryptyxis leesi Pallary, 1928:41, pl. 1, figs a,b. [Dhofar].
Euryptyxis dinshawi Sykes. Connolly, 1931:41. Fisher-Piette & Métivier, 1972:1293, pl. 1, figs 10–13.
Euryptyxis deflersi Jousseaume. Fisher-Piette & Métivier, 1972:1292, pl. 1, figs 18–20.
Euryptyxis latireflexus Reeve. [*pars*]. Fisher-Piette & Métivier, 1972:1294, pl. 1, figs 14, 16.
Euryptyxis leesi Pallary. Fisher-Piette & Métivier, 1972:1295, pl. 2, figs 27–36.
Euryptyxis schoukraensis Jousseaume. Fisher-Piette & Métivier, 1972:1300, pl. 2, figs 24–26.
Euryptyxis socialis Jousseaume. Fisher-Piette & Métivier, 1972:1301, pl. 2, figs 21–23.
Euryptyxis candida Lamarck. Mordan, 1980*b*:106, pl. 1.

TYPE MATERIAL. Lectotype (Here selected, BMNH 1984159) and 2 Paralectotypes (BMNH 1984160) *latireflexus* Reeve, ? Muscat, Oman, Cuming Collection. Two syntypes *lunti* Melvill, Hadramaut, leg. W. Lunt, 1893–4, BMNH 1895.7.10.2–3. Lectotype and 3 Paralectotypes *socialis* Jousseaume, Schoukra, South Yemen, MNHN (selected Fisher-Piette & Métivier, 1972:1302). Lectotype and 2 Paralectotypes *schoukraensis* Jousseaume, Schoukra, South Yemen, MNHN (Selected Fisher-Piette & Métivier, 1972:1300). Holotype *deflersi* Jousseaume, Jebel el Arays, leg. Deflers, MNHN. Holotype *dinshawi* Sykes, Senna, ? South Yemen, leg. E. R. Shopland, BMNH 1903.6.8.7. Six syntypes *leesi* Pallary, Dhofar, Oman, leg. G. M. Lees, BMNH 1928.2.25.1–7.

The type locality of the senior synonym, *latireflexa* Reeve, is uncertain, but clearly that of Muscat given in the *Conchologica Iconica* is erroneous. Specimens closely resembling the types have been recorded from localities as far apart as Qairoon Hairiti, Dhofar (Fig. 28b) and Qubesh, Yemen.

OTHER MATERIAL. **Yemen:** Al Barh, 50 km. W. Taizz, leg. J. Lavranos, 1977, MNHN, (12 specs.), 1978, MNHN, (1 spec.); 45 km. from Taizz, on road to Turba, leg. J. Lavranos, 1978, MNHN, (2 specs.); Marfaq, between Taizz and Hodeida, leg. J. Lavranos, 1978, MNHN, (2 specs.); Qubash, 1700 m, leg. Lavranos, 1979, MNHN (1 spec). **South Yemen:** Hadramaut, leg. W. Lunt, 1893–94, BMNH 1895.7.10.4, (1 spec.), NMW 55.158, (7 specs.); Jebel Jihaf, 7000 ft., leg. H. Scott, ix–x.1937, BMNH, (4 specs.); Jebel Harir, 7500 ft., leg. H. Scott, 4.x.1937, BMNH, (2 specs); Dhala, 1500 m., leg. H. Scott, 12–14.ix.1937, BMNH, (5 specs.) **Oman:** Dhofar, leg. Mrs J. T. Bent, 1894–5, BMNH 1898.12.4.20, (1 spec.); Dahaq Thu'ari, Jabal Qara, leg. C. Bertram, BMNH 1948.5.28.1–5, (5 specs., 2 dissected); Salala, leg. P. Cambridge, 1966, BMNH, (2 specs.); Dhofar, leg. Fuller, iii.1978, ZMC, (3 specs.); Ain Arzat, Jabal Qara, 80 m., leg. P. B. Mordan, 31.v.1976, BMNH 1982, (numerous specs, 10 dissected); Khadrafi, Jabal Qamr, 760 m., leg. P. B. Mordan, 2.vi.1976, BMNH 1982, (numerous specs., 9 in spirit, 3 dissected); Jabal Qara, leg. D. J. Greathead, 3.xi.1976, BMNH, (5 specs.); Wadi Darbat, Jabal Qara, leg. M. D. Gallagher, 20.x.1977, BMNH, (2 specs.); Wadi Sayq, Jabal Qmar, 20 m, leg. M. D. Gallagher, 26.ix.1977, 3.v.1978, BMNH, (5 specs); near Raysut, 100 m, leg. M. D. Gallagher, 6.ix.1977, BMNH, (1 spec.); Wadi Nahiz, Jabal Qara, 500 m, leg. M. D. Gallagher, 27.vi.1977 and R. P. Whitcombe, 21.ix.1979, BMNH, (5 specs.); Tawi Atair, Jabal Samhan, leg. M. D. Gallagher, 9.iv.1977 and 30.iv.1978, BMNH 1982, (numerous specs, 3 in spirit, 2 dissected); WNW Salalah, leg. M. Laferiere, 15.xii.1981, MNHN, (5 specs, 1 dissected); Quiroon Hiriti, Jabal Qara, leg. R. M. Lawton, 9.vi.1982.

DISTRIBUTION (Fig. 17). This species would appear to be the most widely distributed Arabian *Euryptyxis,* extending right across the south of the peninsula from the near the west coast to easternmost Dhofar. It inhabits both coastal and mountainous situations.

DESCRIPTION. Dextral; *globose to elongate conic*; surface with regular radial ribbing, *typically becoming weaker and less regular towards the aperture*, and fine regular spiral striae which cross the ribs; protoconch starting smooth, becoming ribbed; umbilicus closed. Aperture with *well-developed recurved lip*, may be greatly expanded; *strong columellar tooth in body whorl* (Fig. 18A). Colour opaque white to brown, aperture more deeply pigmented.

Shell. Dimensions: Lectotype *latireflexus* Reeve (Fig. 28a): 31·8 × 15·1 × 12·5; 14·9 × 11·1; lip 2·2; 8·2 wh. Paralectotypes: 28·1 × 14·0 × 11·6; 14·0 × 10·6; lip 2·3; 7·9 wh.; 28·9 × 14·0 × 12·1; 13·4 × 10·4; lip 2·2; 8 wh. Syntype *lunti* Melvill (Fig. 28c): 27·6 × 15·2 × 12·0; 14·8 × 11·5; lip 3·1; 8 wh. Lectotype *socialis* Jousseaume: 34·3 × 17·3 × 12·7; 19·2 × 14·2; lip 3·5; 8·1 wh. Lectotype *schoukraensis* Jousseaume: 34·8 × 17·7 × 13·0; 18·7 × 13·7; lip 3·6; 8 wh. Holotype *deflersi* Jousseaume: 30·7 × 16·8 × 12·7; 16·5 × 12·5;

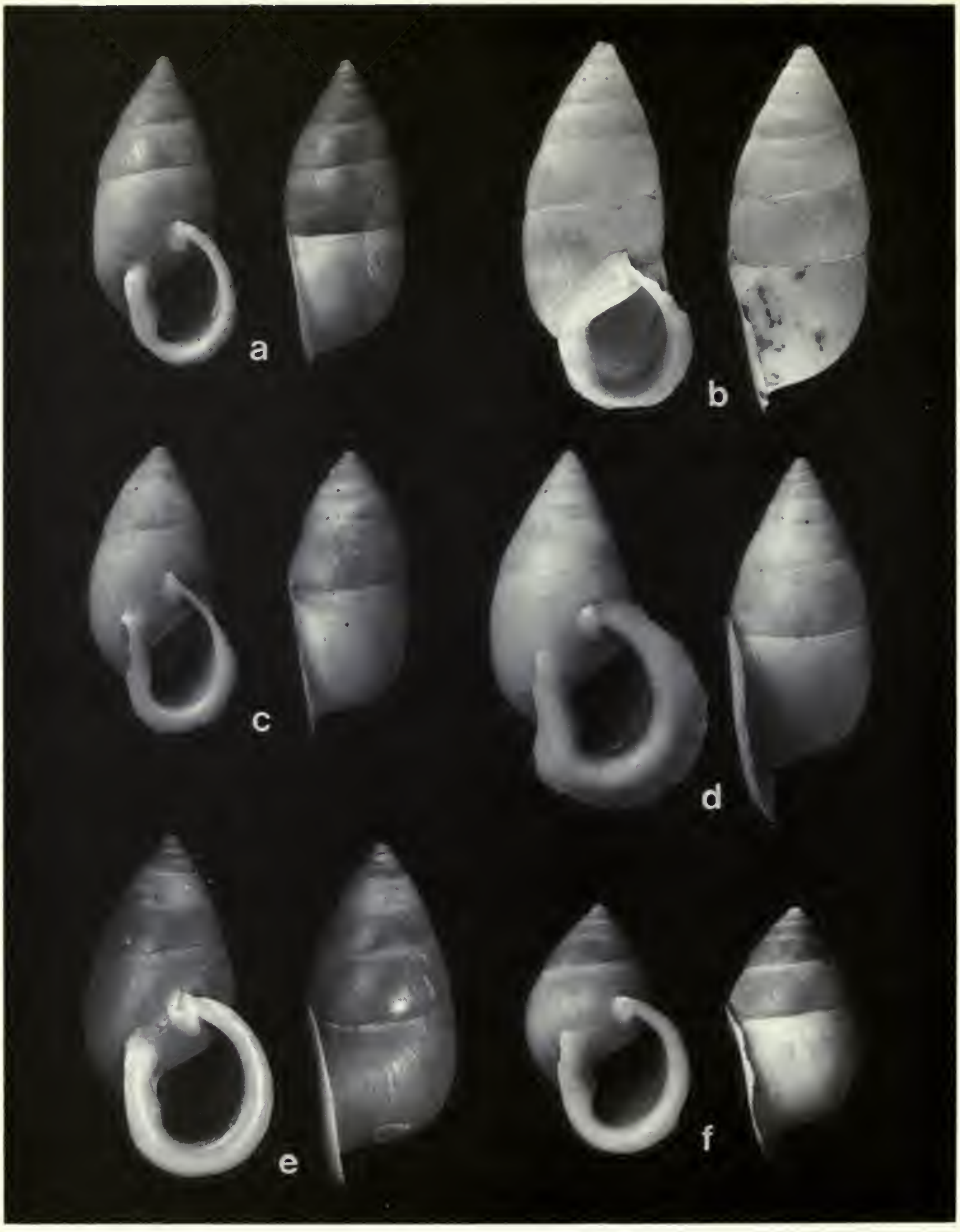

Fig. 28 a, Lectotype of *Buliminus latireflexus* Reeve, BMNH 1984159; b, *Euryptyxis latireflexa*, Qubesh, Yemen, 1979, NMHN; c, figured syntype of *Buliminus lunti* Melvill, BMNH 1895.7.10.2; d, holotype of *Cerastus dinshawi* Sykes, BMNH 1903.6.8.7; e. *E. latireflexa*, Twai Atair, Oman, 1978; f, syntype of *E. leesi* Pallary, BMNH 1928.2.25.1. All × 1·5.

Table 7 Comparison of shell parameters in living populations of *E. latireflexa* from the three principal mountain ranges in Dhofar.

	1. Tawai Atair Jabal Shamhan 30.iv.1978 (n=5)		2. Khadrafi Jabal al Qmar 2.vi.1976 (n=8)		3. Ain Arzat Jabal Qara 31.v.1976 (n=16)		4. Dahq Thu'ari Jabal Qara 27.1v.1977 (n=10)		Anovar 1/2/3	Student's t 3/4	
	x	s.d.	x	s.d.	x	s.d.	x	s.d.	F	d.f.	t
Shell ht.	27·82	1·19	22·18	1·49	26·23	0·81	25·76	2·0	40·59 ***	11	0·17 ns
Sh. max. diam.	16·26	0·35	16·58	0·86	16·94	0·67	15·85	1·1	2·14 ns	14	2·83 ns
Sh. min. diam.	13·48	0·30	13·5	0·89	13·69	0·58	13·59	0·9	0·34 ns	14	0·29 ns
Apert. ht.	15·56	0·81	13·4	0·87	16·36	0·64	15·76	1·28	43·26 ***	12	1·37 ns
Apert. diam.	11·68	0·86	10·44	0·74	13·63	0·62	12·59	1·08	64·14 ***	14	2·77 ns
Spire Index	2·06	0·11	1·66	0·05	1·91	0·1	1·89	0·08	35·70 ***	23	0·81 ns

***p<0·001
ns not significant

lip 2·8; 8 wh. Holotype *dinshawi* Sykes (Fig. 28d): 36·1 × 22·0 × 14·3; 20·7 × 17·5; lip 5·8; 8 wh. Largest Syntype *leesi* Pallary: 27·8 × 17·3 × 13·7; 15·8 × 13·0; lip 3·5; 7·4 wh. Figured syntype (Fig. 28f): 24·7 × 16·0 × 13·5; 15·8 × 13·0; lip 2·7; 7·5 wh.

Shell shape varies considerably within the species, apparently along broad clines. In Dhofar, from where there is a considerable amount of material, statistically significant differences in shell shape were found between roughly contemporary representative samples from the three prinicipal mountain ranges; Jabal Qamar, Jabal Qara and Jabal Samhan (Table 7).

Specimens from Yemen and South Yemen to the west are noticeably more conical than the 'globular' form *leesi* Pallary from Dhofar (Fig. 28f), and often have a very much more developed apertural lip, culminating in the extreme form *dinshawi* Sykes found at Dhala, South Yemen (Fig. 28d).

Body. Pigmentation restricted to tips of tubercles, which are speckled with pale brown; colour darker in head region.

Radula (Figs 26c–f). Table 2 clearly shows distinct differences in tooth size between specimens from Tawai Atair and from Ain Arzat, Dhofar, the former being the larger; it may or may not be significant that at Tawai Atair *E. latireflexa* is sympatric with the smaller *E. labiosa*. Overall radular morphology similar to *E. candida*.

Lung cavity (Figs 29A–B). Kidney of typical orthurethran form, extending from top of lung downwards about 0·75–0·8 times length of cavity (Table 3). Fold of epithelium, up to 1 mm tall, runs from renal pore upwards parallel with kidney almost to top as renal fold, and then reflexes to run downwards alongside rectum as rectal fold. At pneumostome fold turns sharply away from rectum before stopping. Pneumostome fairly complex (Fig. 29B) bearing transverse fold of mantle which emerges from anus. Venation strongly developed, as in other cerastuines. Outer lung wall weakly pigmented with occasional flecks of opaque white.

Reproductive system (Figs 30, 31) Hermaphrodite gland composed of between 5 and 7 irregularly shaped lobes. Albumen gland from 0·5 and 0·8 times length of spermoviduct, and free oviduct about twice length of vagina and two-thirds length of spermatheca. Epiphallus approximately 4 to 5 times length of penis, and only weakly ridged externally; internally with single row of 17 to 28 pits (Fig. 31A; Table 5). Penial caecum conical, varying in height from 0·3 to 0·5 times length of penis; muscular sheath never recurved. Penial and appendicular retractor muscles originate separately on lower lung wall; former divides, two small branches inserting on epiphallus, and main branch on penis proper.

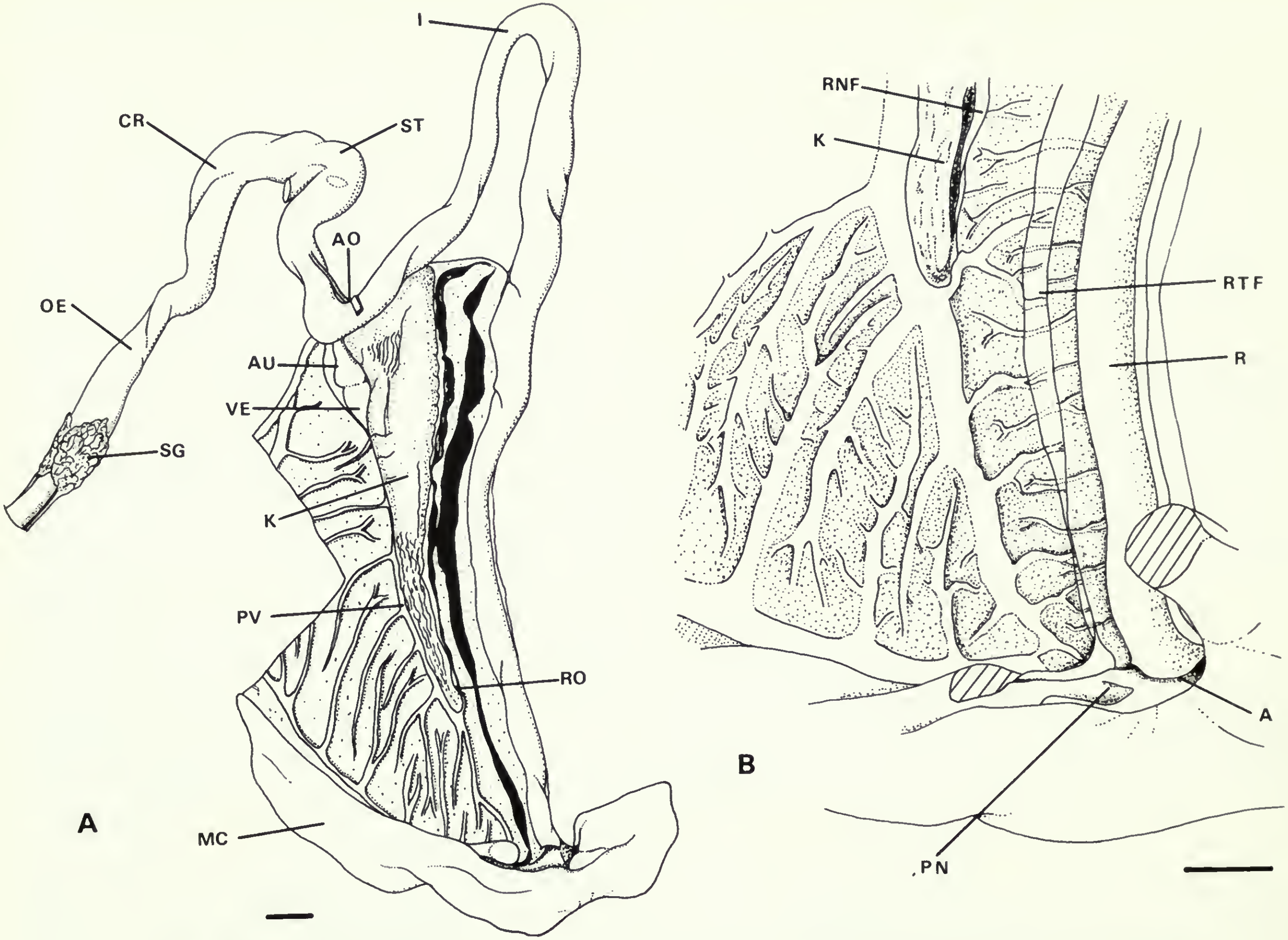
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Fig. 29 *Euryptyxis latireflexa,* Ain Arzat, Oman, 1976: A, lung and alimentary system; B, pneumostome region. Scale 2 mm.

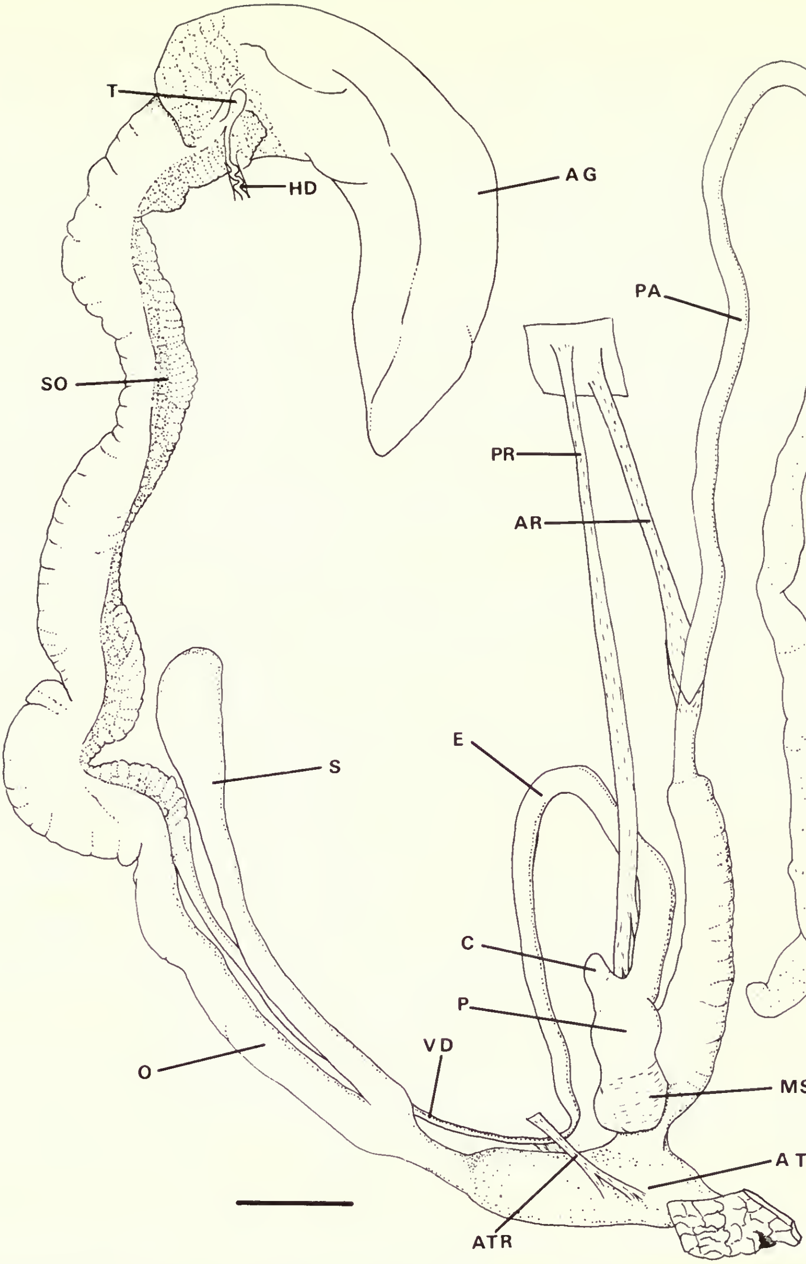


Fig. 30 Genital system of *Euryptyxis latireflexa,* Ain Arzat, Oman, 1976. Scale 2 mm.

Appendix enters penis about one-third the way up and offset from epiphallar pore; its basal region carries 5–6 wavy, longitudinal pillasters, and retractor muscle surrounds lower part of central portion of appendix for a short distance before inserting at its junction with basal region (Fig. 31B). Internal pilaster pattern of penis appears symmetrical (Fig. 31C): on either side of epiphallar pore an elongate glandular area extends upwards almost to top of caecum; just below pore the two fuse for a short distance, only to divide and continue downwards as tapering

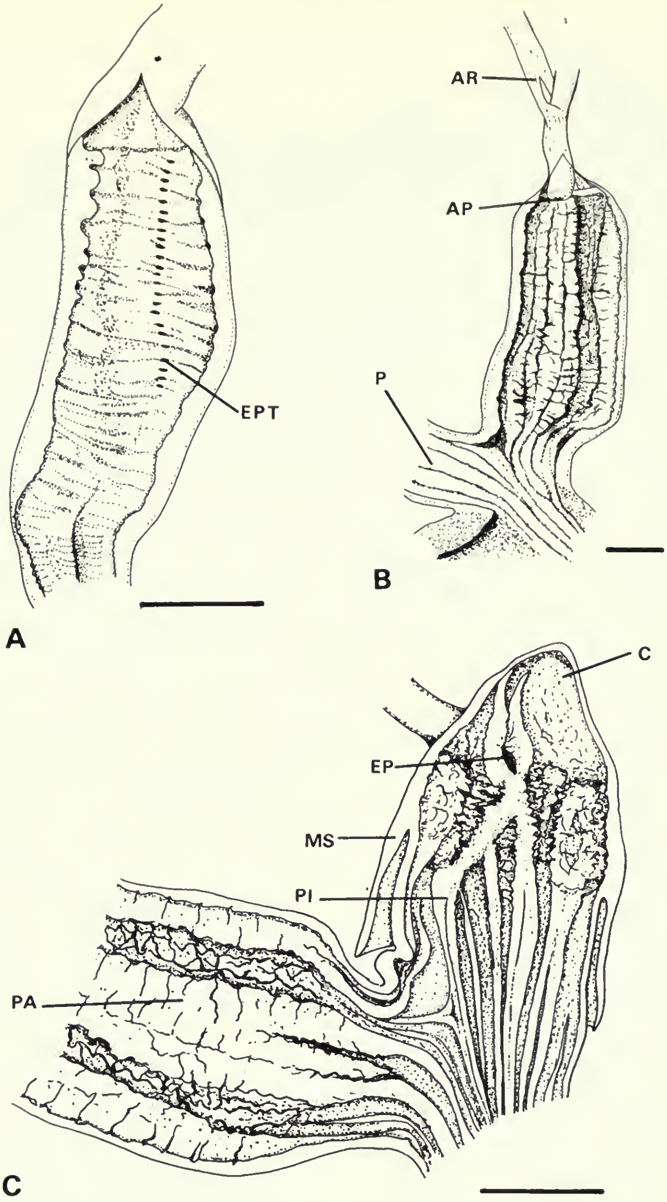


Fig. 31 *Euryptyxis latireflexa*, Ain Arzat, Oman, 1976: A, epiphallus; B, base of penial appendix; C, penis. Scale 1 mm.

pilasters. Also two large glandular patches with associated pilasters, just as in *E. candida*, and one or two intermediate glandular areas.

COMMENTS. *E. latireflexa* as recognised here includes numerous synonyms, and in most cases their present inclusion is based on shell characters alone. Anatomical information is only available from Dhofar, but a detailed study of this suggests that only one species is present there, despite considerable shell variation (Table 7). West of Dhofar there appears to be a clinal increase in shell height and lip width. Although there are a relatively large number of shells recorded from the region of Dhala, the intervening area of South Yemen is poorly known with only the shells collected by Little around Al Mukalla (figured in Pallary, 1925) and Lunt from the Hadramaut (Melvill, 1894).

This species most closely resembles *E. labiosa*. It is however always larger than *labiosa* and differs from it anatomically in the number of epiphallar pits and the relative proportions of the penis, as well as mantle and body pigmentation.

E. revoili Bourguignat from Somalia has a similar number of epiphallar pits to *latireflexa* (Table 5), as well as showing conchological similiarities, but differs significantly in the reproductive anatomy, notably in the insertion of the penis retractor muscle which is on the epiphallus only.

ACHATINELLOIDES Nevill, 1878

TYPE SPECIES. *Bulimus socotrensis* Pfeiffer [monotypy].

DIAGNOSIS. Shell with undifferentiated lip. Penis with short, rounded caecum; penial retractor inserts on epiphallus; appendicular retractor inserts on basal portion of appendix, and originates separatey from penial retractor.

Achatinelloides sebasmia (Jousseaume, 1889)

Ovella sebasmia Jousseaume, 1889:350. [Aden].
Ovella sebasmia Jousseaume, 1890:94, pl. 3, fig. 9–11.

TYPE MATERIAL. 2 Syntypes, Aden, South Yemen, Jousseaume Collection, MNHN.

DISTRIBUTION. Known only from the type locality (above).

DESCRIPTION. Dextral, elongate-conic; surface with regular, coarse, radial ribs, protoconch smooth; umbilicus open. Aperture elongate-oval, lip undifferentiated, thick callus extending across parietal wall and small parietal denticle developed near palatal/parietal border; weak columellar fold. Colour creamy white with irregular, brown, flammulate patterning, weaker on body whorl; protoconch white, sometimes pale brown on lower part of whorl; aperture pale brown internally.

Shell. Dimensions of figured syntype (Fig. 32a): 17·8 × 9·2 × 8·2; 9·6 × 4·8; 7·2 wh. Second specimen immature.

Anatomy. Unknown.

COMMENTS. See under *jousseaumei* below.

Achatinelloides jousseaumei (Jousseaume, 1890)

Ovella jousseaumei Jousseaume, 1890:93, pl. 3, figs 7, 8. [Mahala].

TYPE MATERAL. Syntypes, Mahala, Bourguignat Coll., MNHN, (1 specimen); Aden, Jousseaume Colln. MNHN, (6 specimens).

DISTRIBUTION. Known only from the type material.

DESCRIPTION. As for *sebasmia* above but more globose, with stronger colour patterning on body whorl, and more-developed columellar fold.

Shell. Dimensions of the two mature syntypes (Fig. 32b): 20·2 × 11·9 × 10·1; 11·3 × 6·3; 7 wh. [Bourguignat Colln., possible figure.] 19·4 × 11·0 × 10·1; 11·1 × 6·3; 7 wh. [Jousseaume Colln.] Remaining syntypes immature.

Anatomy. Unknown.

COMMENTS. The genus *Achatinelloides* represents an endemic radiation on the islands of Socotra and Abd al Kuri, with a total of seventeen species being recognised by Smith (1903). They occupy a variety of habitats at elevations up to 1500 m. It is tempting to think of the Arabian specimens as merely introduced Socotran forms because of their highly restricted distribution around the major South Yemen port of Aden, and the similarity of their shells. Certainly *sebasima* is close to *A. balfouri* Godwin Austen, 1881 (dimensions of the figured syntype, BMNH 1881.12.14.20:

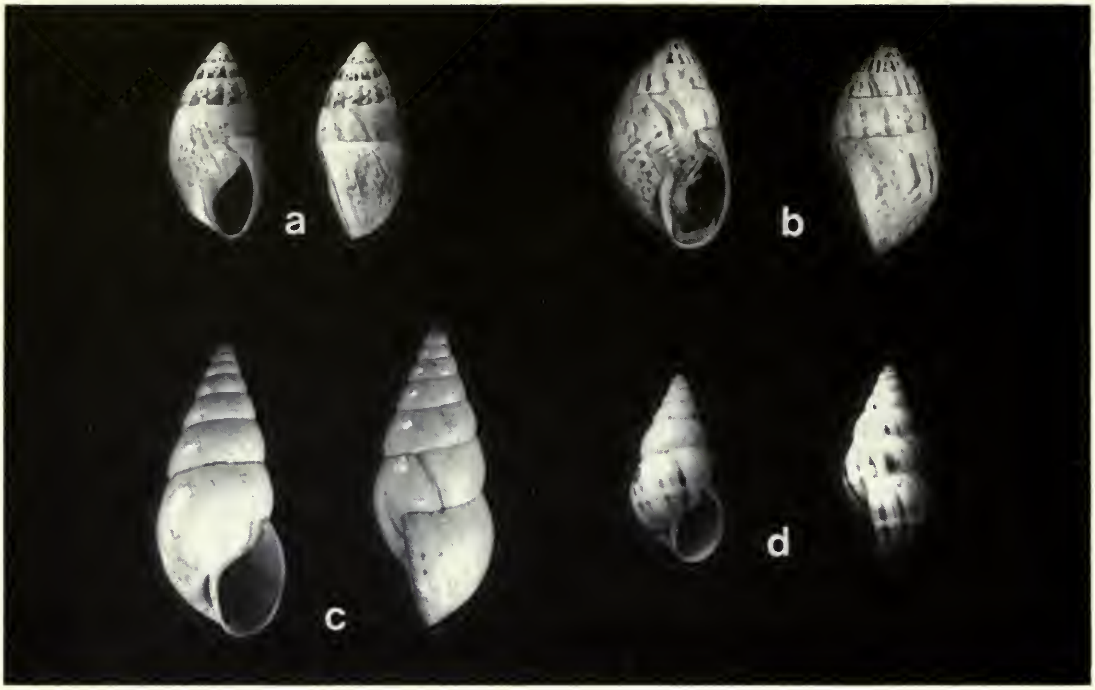


Fig. 32 a, Syntype of *Ovella sebasmia* Jousseaume, MNHN; b, syntype of *Achatinelloides jousseaumei* Bourguignat, MNHN; c, lectotype of *Helix albata* Ferussac, MNHN; d, figured syntype of *Zebrinops ventricosa* Connolly, BMNH 1939.4.19.66. All × 1·5.

20·9 × 10·5 × 10·0; 11·2 × 6·2; 6·7 wh.), and *jousseaumei* is near to both *A. dahamisensis* Smith, 1898 (figured syntype, BMNH 1899.12.20.20: 20·2 × 12·6 × 10·6; 12·4 × 7·3; 6·9 wh.) and *A. homhilensis* Smith, 1898 (figured syntype, BMNH 1899.12.20.51: 19·5 × 11·4 × 10·3; 11·5 × 7·5; 7 wh.).

As the anatomy of *Achatinelloides* has never been investigated, the opportunity has been taken to dissect a poorly preserved aestivating specimen of the type species of the genus, *A. socotrensis* Pfeiffer, 1881, collected on 11.viii.1956 near Hadibu, Socotra (BMNH 1957.7.10.1). The pallial and reproductive anatomy are of the typical cerastine type. The penial and appendicular retractor muscles are separate, but the latter inserts well below the top of the basal portion of the appendix. The penis itself differs from other cerastuines in having three pairs of well-defined longitudinal pilasters in the penial caecum. The caecum is exceptionally thin-walled, the pilaster pattern being clearly visible externally. The penial retractor inserts about one-quarter the way up the epiphallus, which is similar in form to that of *Zebrinops,* and has a single row of approximately 19 internal pits.

ZEBRINOPS Thiele, 1931

Type species. *Limicolaria revoili* Bourguignat [orig. desig.]

Diagnosis. Shell without differentiated lip. Penis with well-developed, elongate caecum; penial retractor inserts on epiphallus. Appendix with long papilla; appendicular retractor inserts on enclosed base of central stalk. Penial and appendicular retractors originate separately.

Zebrinops albata (Férussac, 1827)

Helix (Cochlogena) albata Férussac, 1827:305. [L'Arabie heureuse].
Bulimus albatus Pfeiffer, 1842:42. [Yemen].

Bulimus bicinctus Récluz, 1843*a*:4. [Socotra].
Bulimus albatus Férussac. Küster & Pfeiffer, 1845–55: 225, pl. 62, figs 7, 8.
Bulimus albatus Pfeiffer. Reeve, 1848:pl. ILI, species 333.
Bulimus candidissimus Pfeiffer, 1858:239. [Socotra].
Zebrinops albatus Connolly, 1941:29.
Zebrinops ventricosa Connolly, 1941:29, pl. 3, fig. 15, text fig. 8. [Dhala].
Zebrinops ventricosa Connolly. Fisher-Piette & Métivier, 1972:1302.
Zebrinops albata Pfeiffer. Verdcourt, 1974:5.

TYPE MATERIAL. Lectotype (here selected) and 2 Paralectotypes *albata* Férussac, 'Arabie Hereuse', leg. Rang, MNHN. Syntypes *ventricosa* Connolly, Dhala, South Yemen, 1500 m, leg. H. Scott, BMNH 1939.4.19.66–79, (13 specs).

OTHER MATERIAL. **Yemen:** El Kubar, leg. G. W. Berry, BMNH 1908.2.21.4–9, (6 specs); Nr Ibb, leg. Haythornthwaite, BMNH 1935.4.4.32–33 (2 specs); 2 km N of Taizz, c 1400 m, leg. H. Scott, BMNH 1939.4.19.80–92, (13 specs, 5 dissected); 17 km E of Taizz, 1100 m, leg. H. Scott, 10.x.1937, BMNH, (10 specs); north of Taizz aerodrome, leg. Brunt & Mather, BMNH, (41 specs); Taizz, leg. P. Heath, 1978, BMNH, (5 specs, 3 dissected); Nr. Hammam Ali, leg. Lavranos, MNHN, (1 spec.). **South Yemen:** Hills near Aden, leg. M. J. Ogle, 1.vii.1903, Godwin–Austen Colln, BMNH, (27 specs); Dhala, leg. Meinertzhagen, xi.1948, BMNH 1954.4.5.1–5, (5 specs).

DISTRIBUTION (Fig. 33). Almost all the material examined originates from two principal areas: the environs of Taizz in North Yemen and Dhala in South Yemen. This may well represent collecting bias, but interestingly the former represents typical *albata* whilst the latter material is largely referable to *ventricosa*. Additional material from near Aden and from Al Kubar, to the south and east of Dhala respectively, is of the *ventricosa* type.

DESCRIPTION. Dextral; elongate conic; umbilicus narrow and shallow. Protoconch smooth; subsequent ornamentation consists only of weak growth lines and occasional malleations; texture glossy. Colour of protoconch often light to dark brown, may be white, remainder opaque white with two interrupted spiral bands of brown (the lower only visible on body whorl) which may extend radially as streaks.

Shell. Dimensions of lectotype (*albata* Férussac) (Fig. 32c): 26·3 × 11·4 × 10·6; 10·1 × 6·6; 8·9 wh. Paralectotypes: 24·6 × 11·3 × 10·0; 10·3 × 6·2 × 8 wh.; 22·5 × 11·3 × 10·6; 9·5 × 5·5; 8·4 wh. Dimensions of figured syntype (*ventricosa* Connolly) (Fig. 32d): 16·6 × 8·3 × 7·5; 6·7 × 4·6; 7·5 wh. Dimensions of largest complete specimen, Taizz, leg. Brunt and Mather: 35·2 × 16·5 × 15·7; 15·0 × 9·5; 9·6 wh.

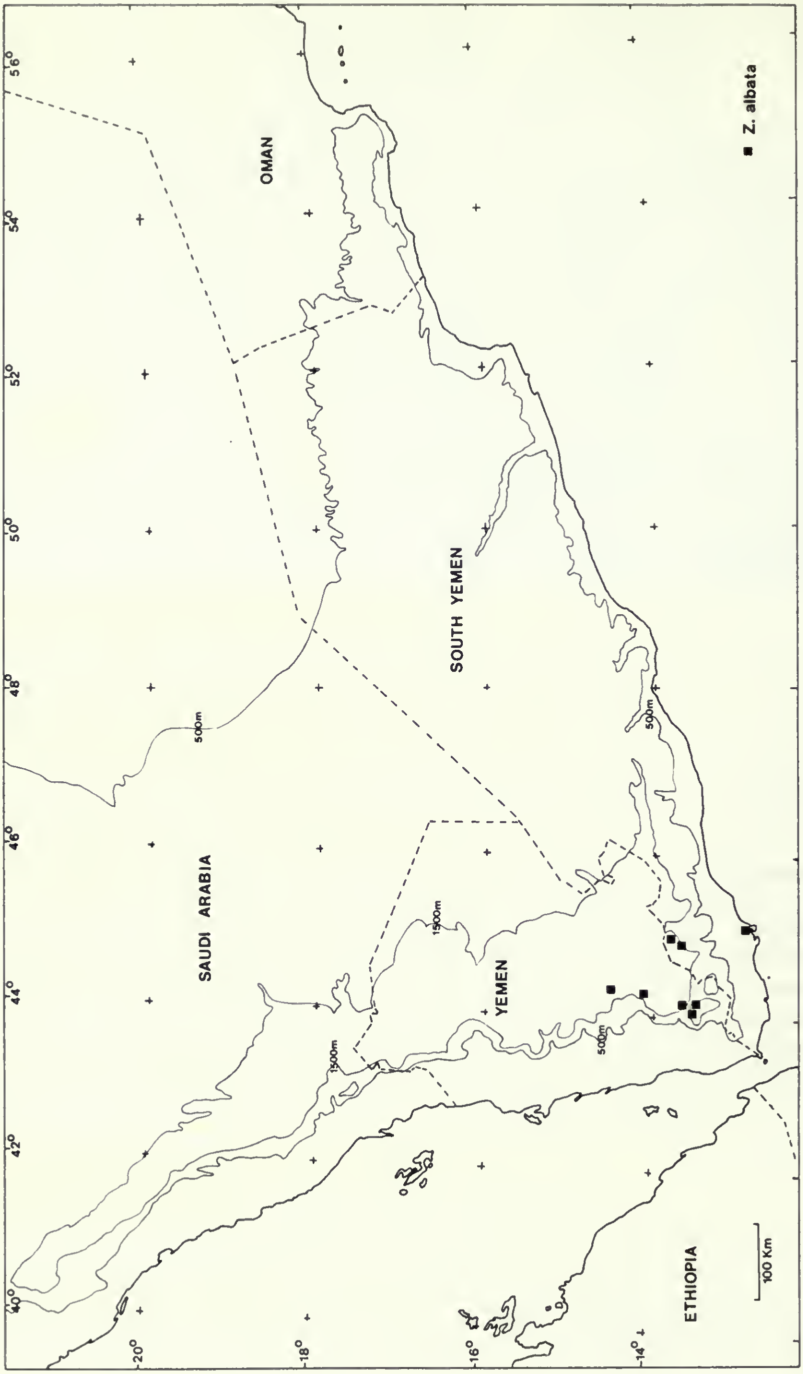
The specific distinction of *ventricosa* was justified by Connolly largely on conchological grounds, principally shell size and shape, but this does not seem to hold up to analysis. The sample collected by Hugh Scott from 2 km north of Taizz comprises mainly good *albata*, but also includes a few smaller specimens. Height against whorl number of this material is plotted in fig. 34, and it can be seen that the two show a clear linear relationship. Additionally, the type specimens of *albata* and *ventricosa* are included in the plot and tend to confirm that the two nominal taxa merely represent age classes of the same species. A statistical comparison of the type series of *albata* and *ventricosa* in respect of the H/D ratio of the shells failed to demonstrate that the latter were significantly more ventricose (Student's t test: 18 degrees of freedom, $t = 0{\cdot}973$, not significant).

Body. Generally pale, becoming darker towards head region.

Radula (Fig. 35). Both radulae examined extremely worn in central and lateral areas, but marginal teeth in good condition. In all except first two or three marginals of row, ectocones multicuspid. Tooth dimensions and numbers given in Table 2.

Lung cavity. Of typical cerastuine type with well-developed complete renal and rectal folds and prominent venation. Kidney 0·85 times the length of lung. Outer wall clear and unpigmented in most individual, but some have distinct pigmentation in pneumostome region and along rectum.

Reproductive system (Figs 36, 37). Hermaphrodite gland composed of 5 to 6 lobes, and talon sharply curved (fig. 36A). Albumen gland large, approximately 0·9 times length of spermoviduct; latter wider, relative to its length, than in *Euryptyxis,* as is spermatheca which has distinctly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48°
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OMAN
SOUTH YEMEN
SAUDI ARABIA
YEMEN
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500m
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500m
1500m
1500m
■ Z. albata
100 Km

Fig. 33 Distribution map of *Zebrinops albata*.

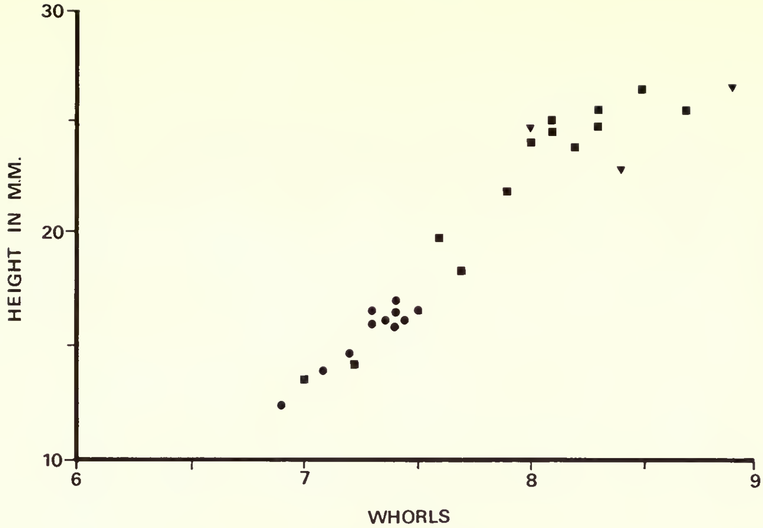

Fig. 34 Plot of shell height (in mm.) against whorl number for three samples of *Zebrinops albata*. Triangles: type series *Helix albata* Ferussac, Arabia; circles: type series *Zebrinops ventricosa* Connolly, Dhala, S. Yemen; squares: 2 km N. Taizz, Yemen, leg. H. Scott, 10.x.1937, BMNH.

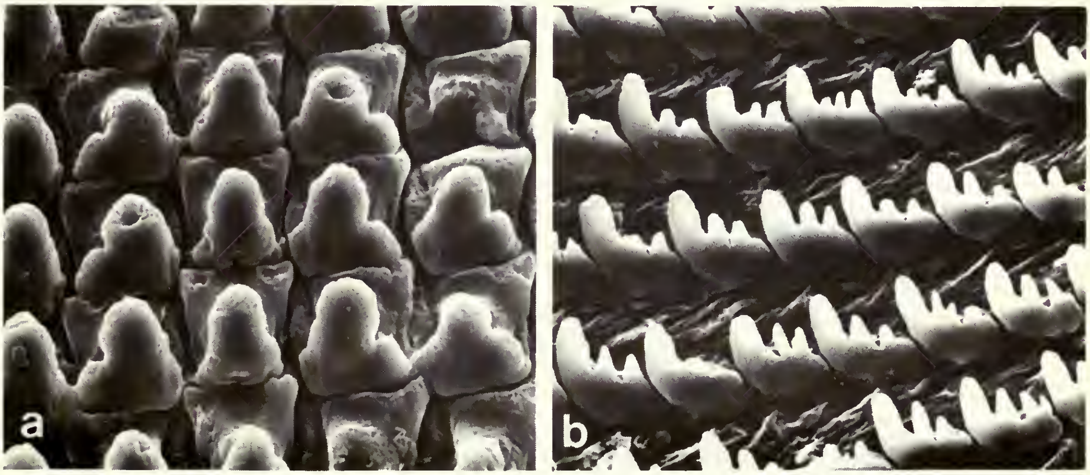

Fig. 35 Radula of *Zebrinops albata,* Taizz, 1978: a, central and lateral teeth; b, marginal teeth; magnification × 720.

globular head. Short spermathecal stalk bears between six and eight strong longitudinal pilasters internally.

Epiphallus massively expanded compared to vas deferens, and bearing longitudinal row of 20–22 strong transverse ridges, the strongest of which are closest to penis and of 'dumbell' shape. These correspond to equivalent number of internal pits (Figs 37B,C), and to spines on spermatophore (Fig. 9A). Penis retractor unbranched and inserts on epiphallus well above penis junction. Externally, penis characterised by large, thick-walled caecum which is as long as penis itself. Internal structure of penis relatively simple (Fig. 37D). Transverse groove at level of

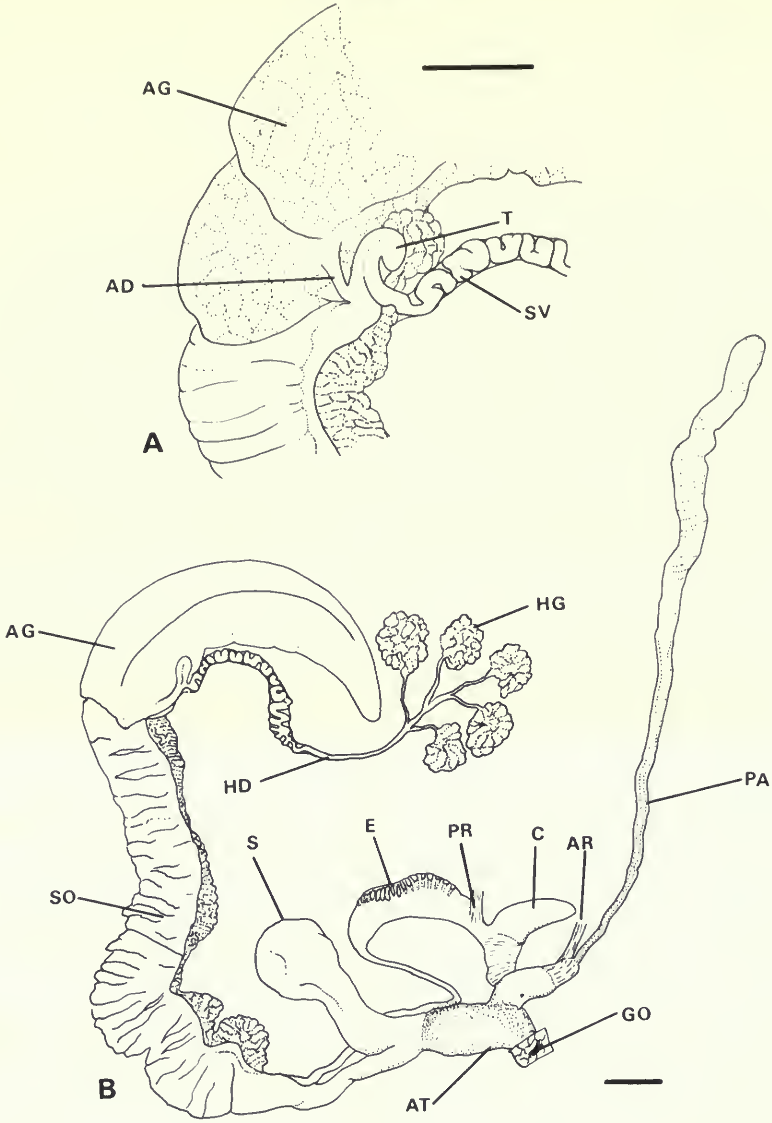

Fig. 36 *Zebrinops albata,* Taizz, Yemen, 1978: A, talon region; B, genital system. Scale 1 mm.

epiphallar pore separates caecal area (which bears numerous small, oval glandular patches) from main body of penis which bears 9–10 equal longitudinal pilasters. Penial sheath single-layered.

Appendix inserts broadly on penis below epiphaller pore; short basal portion with regular longitudinal pilasters, and basal part of middle region enclosed by hollow muscular sheath formed from retractor muscle; central stalk projects downwards through septum into lumen of base as long, fine papilla (Fig. 37D).

Comments. There does not appear to be any conchological or anatomical justification for the separation of *albata* and *ventricosa* and therefore the two names are synonymised. The smallest specimen dissected was sexually mature and had a shell height of only 14·2 mm and 7·0 whorls, suggesting that in this group growth is probably not determinate. A number of continental African *Zebrinops* have been dissected and all clearly belong to species other than *albata.*

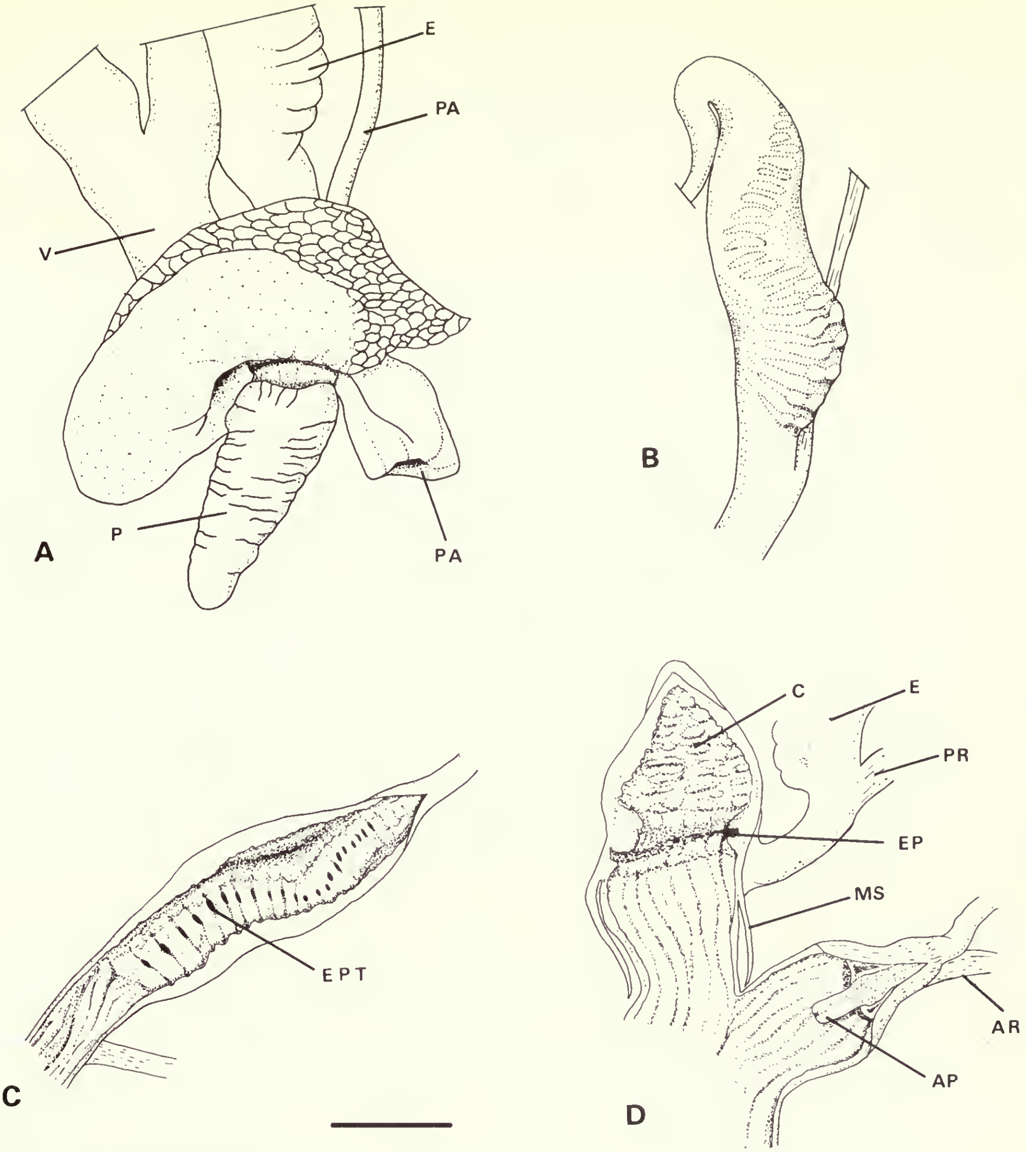

Fig. 37 *Zebrinops albata* Taizz, Yemen, 1978: A, everted genitalia; B, epiphallus, external; C, epiphallus, internal; D, penis and base of appendix. Scale 1 mm.

Discussion

The following discussion addresses two, essentially distinct problems involving decisions made at different taxonomic levels: the problems of species discrimination in arid-habitat land snails; and secondly a consideration of the differences which have been shown to exist between the two major family-group taxa, the Enidae *sensu stricto* and the Cerastinae.

Discrimination at the species level

Shell characters, and more recently characters of the terminal genitalia, have been used to discriminate species of land snails. The former are clearly subject to the effects of environmental variation, but the relationship between the latter and possible species-isolating mechanisms would appear to be a direct one. Certainly the genitalia have been found pragmatically to be useful in providing low-level taxonomic characters in pulmonates, as well as other animal groups (Arnold, 1973). However, Mayr (1963:103) discounts the importance of mechanical isolation in most cases, suggesting that the observed differences in genital structure are the result of pleiotropy. A possible mechanism by which such pleiotropic changes could be stored by the genitalia, rather than be eliminated by normalizing selection as in other organ systems, has been explored by Arnold (1973, 1983).

Clearly information on soft anatomy is desirable wherever possible, but despite examination of almost all the Arabian pulmonate material currently available in museums, most or all Arabian species in the genera *Cerastus, Achatinelloides, Paramastus* and *Polychordia* are known only from shells, and even for species whose internal anatomy is known, our principal information regarding their geographical distribution and variation is derived from shell collections. Nevertheless, morphological groupings based on shell characters have emerged which are consistent with the limited anatomical information available, and consequently must be regarded as species. The level of confidence in the taxonomy presented here varies greatly between taxa: in the case of the northern Oman enids it is high, for living material was available from a relatively large number of sites throughout the known geographical range, but is much lower in groups such as *Euryptyxis* which are conchologically highly variable and for which anatomical information is available from only a limited part of their assumed distribution.

The high levels of shell variation, so characteristic of many desert groups, stem primarily from two factors: the extreme climatic variability, both spatial and temporal, characteristic of desert environments, and the genetic isolation resulting from the wide separation of most of the populations, often combined with small population size. Reduced gene flow between populations will be accentuated in the larger pulmonate snails considered here, where vagility is reduced further by their habit of aestivating for most of the year attached to rocks or trees, and the analogy has been drawn between the genetics of such semi-sessile animals and that of plants (Selander & Hudson, 1976). Moreover, in periods of extensive mortality these various factors may combine to produce a temporal form of genetic drift, the 'bottle-neck' effect (Cain, 1983), which can cause local fixation of the genotype into a new mode.

Family-level groups

The elucidation of higher-level taxonomy typically requires different, or at least additional characters to those used at the species level, and in this study the pallial cavity and proximal genital system (proximal to the gonad) have been found to be of particular value. Two family-level groups are here defined for the purposes of the discussion: the Enidae *sensu stricto* (comprising the nothern families Eninae and Chondrulinae, *sensu* (Forcart, 1940); and the Cerastinae (or Pachnodinae) *sensu* Zilch, 1959). Any subsequent unqualified use of the term Enidae refers to the former group alone. Consideration of the relationships within the Cerastinae will be deffered until an anatomical study of all the component genera has been completed, and a phylogenetic analysis can be undertaken (Mordan, in prep.).

In the remainder of this discussion, the characters studied are considered system-by-system, rather than in terms of their value at the various taxonomic levels.

Shell

Limited information on shell variation is available for some living populations from Dhofar and northern Oman, where the greatest collecting effort was directed. However, no detailed statistical analysis of shell form and its possible correlation with environmental variables has been attempted, partly because of the lack of an adequate range of sufficiently large samples. Also, no climatic or vegetational data are available for the relevant areas (see Taha *et al.*, 1981, for a summary of Arabian climate). Assemblages of dead shells are generally unsuitable because of uncertainty of their provenance owing to the possibility of passive transport, and even living populations, at least of some species, appear to comprise adults from a number of year classes which may themselves vary (see below).

Woodruff (1978) has summarised knowledge of variation in the shells of *Cerion*, a West Indian genus with a ecology in many respects similar to the Arabian species, and many of the points he made are relevant to the present discussion. Woodruff considered the shell under the following headings, which for convenience are used here:

Shell size and shape

Populations of all species appear to vary considerably in size of both the adult shell and the aperture, and this is known to be correlated with climate in some other land snail groups (Heller, 1975; Woodruff, 1978; Tillier, 1981). Subtleties of shape are more difficult to quantify accurately, and here the simple height/diameter ratio (the spire index of Cain, 1977) is used; in the subsequent discussion 'shape' refers to this parameter.

Spatial variation in both size and shape is demonstrated in *E. latireflexa* from Dhofar, where roughly contemporary (1976–78) living samples are available from each of the three principal mountain ranges: Jabal Qamar, Jabal Qara, and Jabal Samhan. Analysis of variance shows highly significant inter-population variation in shell height and aperture size between the three mountains, whereas comparison of two living samples from separate sites within the Jabal Qara range shows no such differences (Table 7). Concomitant changes in shape are also recorded between the three mountains, with significantly more globose forms (*leesi* Pallary, Fig. 28f) in Jabal Qamar; as with size, there is no significant difference between populations within the Jabal Qara range (Table 7). This variation may be viewed in a number of ways: as vicariant, in the sense that topography has divided the species into a number of allopatric units which are starting to diverge morphologically, or as points on a cline of increasing shell size running west to east in Dhofar. If the latter is true then the cline reverses for, on the evidence of dead shells, both height and spire index increase westwards from Jebel Qamar, culminating in the form known as *dinshawi* Sykes (Fig. 28d). Alternatively, the observed inter-population differences could be purely random.

Populations of *E. candida* on the Red Sea island of Dumsuk, in the Farsan group, and from the coastal Tihama of Saudi Arabia and Yemen are noticeably smaller than the more typical populations at higher elevations where rainfall is greater, approaching the size of *E. labiosa* (a small, essentially coastal species, which also occurs on Dumsuk). Shell size and shape are also compared in living populations of *Mastus omanensis* and *Imparietula jousseaumei* in N. Oman; in the former no highly significant differences were found (Table 1), but in *I. jousseaumei* significant results have been obtained for all parameters, particularly for shell diameter and spire index (Table 4). Unusually elongate forms of *jousseaumei* were collected from a remote gorge on Jabal Sira (part of Jabal Akhdar, N. Oman) at an elevation of 2400 m. This may simply be part of the general trend for increasing spire index with elevation in this species, but *Pupilla c.f. annandalei* Pilsbry also occurs at this site (the species is otherwise known only from the type locality in Nepal) suggesting perhaps a long-isolated relict fauna in the area (Mordan, 1980*b*).

Temporal variation in size, but not shape, is also evident in some populations. Significant differences are found for all size parameters (excepting lip width) in comparisons of living and very recently dead shells with shells which had been dead at least one dry season, from a single sample of *Euryptyxis labiosa* from Jabal Samhan, Dhofar. No significant differences exist between the living and freshly dead samples (Table 6). Climate, and in particular precipitation, varies considerably from year to year so that size variation between age classes is not at all unexpected; feeding activity, and thus shell growth, is known to be highly correlated with soil moisture levels in desert snails (Shackak, Orr & Steinburger, 1975).

Shell shape formed the basis of Connolly's separation of *Zebrinops ventricosa* from *Z. albata* (Connolly, 1941), but a statistical comparison of spire indices of the two type series failed to separate them. Similarly, a plot of shell height/maximum shell diameter for the types and a relatively large sample from Dhala, S. Yemen suggests that all form part of a continuous growth series (Fig. 34).

Certain aspects of shape which the spire index fails to distinguish may be useful in separating closely related species: in particular *Euryptyxis fragosa* and *E. candida,* which commonly co-occur in SW. Arabia, differ in the curvature of the sides of the spire profile, the former being more or less flat from the apex down to the body whorl giving a conical profile (Figs 16e–g), the latter markedly convex between the nepionic and body whorls (Figs 16a–d). *Eyryptyxis candida* in particular shows clear ontogenetic shape changes similar to those described by Cain (1981) for certain *Cerion* species, but knowledge of *Euryptyxis* ecology is insufficient to make any suggestions regarding possible adaptive values.

Lip size and shape

Lip expansion is known to be inversely correlated with moisture in some desert snails (Heller, 1975; Woodruff, 1978), and varies greatly between Arabian cerastine species. Although there is no thickening of the lip region in any species, other than the general thickening of the shell which occurs with age in many pulmonate groups (Pollard, 1975), the degree of lip flare or curvature proved a valuable diagnostic character at both generic and specific levels. No lip differentiation is found in either *Zebrinops* and *Achatinelloides,* and is only weakly developed or absent in *Cerastus.* The absence of a differentiated lip makes it impossible to establish maturity from the shell alone, but does not necessarily imply that growth is indeterminate.

Mature *Euryptyxis* always develop a lip, although this ranges from a simple flairing of the aperture in *E. candida* and *E. fragosa* (Figs 16a–g) to a truly recurved structure in *E. labiosa* and *E. latireflexa* (Figs 25, 28). In this last species, the lip can become greatly expanded in some western populations (described under the name *dinshawi* Sykes). The apertural region appears to thicken progressively in most adult snails, and under suitable conditions this could give rise to such extreme lip development. In *Euryptyxis* overall thickening of the shell with age in certain geographical regions also appears to correlate positively with the degree of development of the columellar fold, although there do appear to be overriding intrinsic differences in the size of the fold between individual species (Fig. 18). Both enid species develop lips as adults, but *Mastus omanensis* shows a greater degree of variation in this respect, with one specimen from Qasaydot, Jebel Harim, N. Oman, having an exceptionally expanded lip reminiscent of the *dinshawi* form of *Euryptyxis latireflexa.*

Shell sculpture

This again proved a valuable character in determining species of *Cerastus* and *Euryptyxis.* Of particular value was the relative development and regularity of radial ribbing, and in the case of the latter genus, the extent of development of spiral striae. Three of the species of *Euryptyxis* showed the development of very coarse ribbing in some populations which has given rise to a number of new names from Bourguignat and Jousseaume, but on the evidence of dissections of both smooth and ribbed forms of *E. fragosa* from Taizz, Yemen, such variation comes within the limits of the species as recognised here.

Apical shell sculpture of all species was examined under the stereoscan microscope but showed no taxonomically valuable characters.

Visceral mass

There is considerable variation in the absolute and relative proportions of the shell and visceral mass between genera, expressed in terms of whorl number. Table 3 shows typical lengths of the three principal regions of the visceral mass: the mantle to the top of the lung; the top of the lung to the top of the stomach; and the region above the stomach, which is composed of the posterior lobe of the digestive gland and contains the gonad.

In all genera it is clear that the total visceral mass does not extend to the apex of the shell, and in many species the apical shell whorls are sealed off internally by a septum. In the more-elongate genera *Imparietula* and *Zebrinops* the visceral mass extends relatively further towards the apex than in the shorter forms where the differential between shell and total visceral mass may exceed three whorls. The observed differences between species with elongate and short shells appears to be accounted for by the greater length of the region above the stomach in the former although additionally the lung of *Imparietula* extends almost two whorls, compared with about one whorl for the other taxa. On the evidence from the species examined, variation does not seem to correlate with family-level groupings.

Alimentary system

Radula

In all species for which there was anatomical material available the radula was examined but little useful information emerged. It is significant that in recent taxonomic revisions of genera in both the Enidae (eg. Heller, 1974; 1975) and Cerastinae (eg. Verdcourt, 1966, 1970; van Mol & Coppois, 1980) the radula has not been used as a diagnostic character at either specific or generic levels. The results are summarized in Table 2.

In *Euryptyxis* both tooth size and number were generally fairly uniform between the three larger species, but in the smallest, *E. labiosa*, where overall radula size was smaller, tooth number, but not size, was distinctly reduced. In *Cerastus* the number of teeth was much as in *Euryptyxis*, but the teeth were generally smaller and the difference in size between the centrals and laterals more pronounced. In *Zebrinops* and *Cerastus* tooth number appeared to vary with size. The radula formula of both enid species was similar, but interestingly the size of individual teeth in *Mastus omanensis*, the larger species, was approximately twice that of *Imparietula jousseaumei*.

At higher taxonomic levels there appear to be no consistent differences between the radulae of many orthurethran groups, although some authors, for example Solem (1962), have referred to a characteristic 'enid' radula. Watson (1920) pointed out the close similarities between the enid radula and that of other Pupillacea, and referred to a generalised radular type characteristic of 'the less-specialised members of the Orthurethra'. This has rows possessing a symetrically tricuspid central tooth with a large, usually pointed, mesocone and markedly smaller outer cusps, and bicuspid laterals with a reduced ectocone, which are typically larger than the central tooth. The marginal mesocone is often very blunt and the ectocone typically with a single cusp which becomes progressively more subdivided towards the edge of the radular row. In particular, there seem to be no reliable radular differences between the Enidae and the Cerastinae. Both Watson and Steenberg, in separating the Cerastinae (=Pachnodinae of Steenberg, 1925) from the Enidae, made much of the distinctly angled disposition of the tooth rows in *Pachnodus*. However this genus is clearly specialised in its dentition, being arboreal, and is not typical of the family as a whole (see for example *Euryptyxis fragosa*, Fig. 19e); such radular modifications to an arboreal mode of life have been shown to be convergent in a number of cerastines (Solem, 1973). The total number of teeth in a row is normally higher in the Cerastinae than in enids and the latter group never approaches the total of 463 teeth recorded by van Mol & Coppois (1980) for *Pachnodus velutinus* Pfeiffer. An analysis of enid tooth number from Hesse's review of the family (Hesse, 1933) shows an average number of 62 (s.d. 17·7; range 29–107) teeth per row.

Crop and Intestinal Folds

Beck (1912: pl. 9, fig. 23.) illustrated the internal structure of the stomach region of *Zebrina detrita* Müller, clearly showing two longitudinal crop folds passing posteriorly to the digestive gland ducts, and two intestinal folds running posteriorly from the ducts to the small intestine. It is evident from Beck's figure that, as in Arabian *Mastus* and *Imparietula*, the intestinal fold emanating from the posterior duct opening is more highly developed than that coming from the anterior duct, and in the Arabian enids it develops into a true flap which extends some distance along the intestine. This is in marked contrast to the cerastines *Euryptyxis* and *Zebrinops* where both intestinal 'folds' are little more than thickenings of the epithelium. The paired crop folds are similarly reduced, and are often barely visible. Such differences are of potential taxonomic significance, but require more-detailed investigation.

Lung cavity

Lung folds are more highly developed in the Cerastinae than in any orthurethran group. A short renal fold is found in some Eninae (Weigmann, 1901; Beck, 1912) and Chrondrulinae (pers. obs.), as well as certain Pupillidae (Steenberg, 1925), but apparently occurs in all cerastines. Typically it extends the full length of the kidney, and in *Amimopina* (Solem, 1964) and a number of African cerastine genera (pers. obs.) is closed throughout its length, giving rise to the 'pseudosigmurethrous' condition described by Solem (1964); a similar arrangement was also reported for *Acanthinula aculeata* by Watson (1920). In cerastines the renal fold normally joins the rectal fold at the apex of the pallial cavity, the latter then extending downwards to the pneumostome. In juvenile *Euryptyxis* the rectal fold was found to extend down only to the level of the tip of the kidney, but is fully developed in the adult. Rectal folds are found in all Arabian genera, *Pachnodus* (van Mol & Coppois, 1980), *Rachis* (Seshaia, 1932), *Amimopina* (Solem, 1964), as well as *Conulinus, Rhachidina* and *Rhachistia* (pers. obs.). It is known to be lacking only in *Edouardia* (Connolly, 1925; and pers. obs.).

The lung folds of cerastines serve to partition the lung cavity into functionally distinct respiratory and excretory areas, and this is correlated with the development of prominent pallial venation, particularly of the respiratory area. By contrast, no vessels are macroscopically visible on the outer lung wall of enids. Tillier (1982) concluded that in slugs an extensive lung vascularisation increased effective respiratory surface area, and is developed in response to a reduction in lung size. Whilst the cerastine lung is not relatively shorter than in many enids (Table 3), its respiratory area is reduced laterally by the lung folds. Differences in size between the vessels of the lung wall and those within the folds, which are typically narrower, were also noted and may be related to the differing functions of the two areas: the large vessels may, for example, serve to increase the blood supply to resorbtive region of the lung, which would potentially be of great importance in xerophilic taxa. The groove clearly has a resorbtive function in cerastines, as van Mol & Coppois (1980:22) have described a well-developed brush border epithelium in the renal groove of *Pachnodus*.

Reproductive system

Hermaphrodite Duct Diverticulae

These structures were first described from *Ena* and *Zebrina* by Martens & Wiegmann (1898:82), who also pointed out that they were absent from *Pachnodus;* subsequently Wiegmann (1901:282, pl. X, figs 12 & 23) figured similar structures from *Subzebrinus*. Hesse (1933:154) also figured the diverticulae in *Chondrula* and their taxonomic importance was discussed by Steenberg (1925) who referred to them as *culs-de-sac*. They are presented in both Arabian enid species but are absent from the cerastines, and take the form of a clump of blind-ended sacs situated on the hermaphrodite duct between the hermaphrodite gland and the seminal vesicles (Figs 7A, 8B–D, 11A). Their function is unknown although Wiegmann noted that they contained sperm. They are not known from any other Stylommatophora, and appear to form a synapomorphy separating the Enidae from other Orthurethra. Similar-looking structures have been reported in certain Basommatophora by Hubendick (1978) who referred to them as seminal vesicles; whether or not these are homologous with the stylommatophoran seminal vesicles as defined by Bayne (1973) is unknown. What is clear is that the Enidae possess a true seminal vesicle (*sensu* Bayne) in addition to the *culs-de-sac,* suggesting that the latter might be an independent structure formed *de novo*.

Spermoviduct

On the basis of a figure and description in Beck (1912:223, pl. 9, fig. 31), Steenberg (1925) has stated that the enid spermoviduct is differentiated into three grooves; he had earlier described a similar organisation in the Clausiliidae (Steenberg, 1914), and was later to record the presence of this third groove in the Pupillidae (Steenberg, 1929). A similar configuration is found in northern Oman enids. Steenberg referred to this third groove as the 'serous canal' and suggested that it originated from the oviducal portion of the spermoviduct. In cerastines the organisation is different: van Mol & Coppois (1980) described only two grooves in *Pachnodus*, a spermiduct and an oviduct, agreeing with my own histological observations on *Euryptyxis* and *Zebrinops*.

Visser (1977) has recently reviewed the systematic importance of the spermoviduct in the Pulmonata, and although he tentatively included the Clausiliidae in his 'incomplete triaulic' category, I consider that Steenberg's observations on the clausiliids are better interpreted as the 'semi-diaulic' condition, as the serous canal remains a groove throughout its length, never separating as a free duct. Visser recognised two principal lineages in the Stylommatophora, both containing groups showing the semi-diaulic, monotrematic condition, but apparently differing in the homology of the free male duct (vas deferens). Group A, where the vas deferens forms from the sperm groove, included the Clausiliidae (the 'serous canal' is presumably equivalent to Visser's 'seminal groove' which serves to transport exogenous sperm). Group B incorporates some Pacific Orthurethra (Achatinellidae) and the Succineidae and is characterised by a vas deferens originating from the seminal groove.

Although both the Enidae and the Cerastinae are at Visser's semidiaulic level of organisation and would appear to fall within the stylommatophoran group A, they clearly differ fundamentally by the presence of a third spermoviducal canal in the former. Visser (1977:48) admits that 'two morphologically widely divergent types of reproductive system as displayed by (i) *Achatina* and (ii) *Agriolimax*' are included under the semi-diaulic designation in group A. The differences between the spermoviducts of enids and cerastines are analogous with those of Visser's examples: *Achatina* with a spermoviduct 'consisting of a female channel, a sperm groove and a seminal groove', and *Agriolimax* where 'the spermoviduct consists solely of a female channel and the sperm groove'.

Terminal Genitalia

It is generally recognised that the terminal genitalia of land molluscs provide a rich source of taxonomically important information below the family level (Solem, 1978), and Cain (1982) referred specifically to gastropod genitalia in exemplifying what he termed 'privileged characters' in a taxonomic sense.

Some useful family-level characteristics also are to be found in the terminal region, particularly in the Cerastinae where the overall pattern appears to be remarkably constant. A highly characteristic brown spongy tissue is found lining the atrium and vagina of most cerastines. This was first noted by Seshaiya (1932) in *Rachis,* but is also present in *Amimopina* (Solem, 1964), *Pachnodus* (van Mol & Coppois, 1980), *Euryptyxis, Cerastus, Zebrinops, Acatinelloides, Edouardia, Rachistia,* and probably most other members of the subfamily; the only group for which it has been noted as absent is in central African *Cerastus* (Verdcourt, 1970). The histology has been described by van Mol & Coppois (1980), who noted the presence of melanin and elastic fibres in the cells, and similar tissue has not been described in any other group. Additionally, a spermatheca lacking a diverticulum is always developed, and typically joins the free oviduct close to or at the commencement of the melanic tissue.

Of particular interest within the Orthurethra is the development of a penial appendix. An appendix with a remarkably uniform basic structure is found in many pupillacean groups in addition to the Enidae and Cerastinae: the Achatinellidae, Orculidae, Cionellidae, Amastridae, Pupillidae, Vertiginidae and Valloniidae. It seems probable that it is homologous within these various groups, and its presence defines Shilieko's suborder Pupillina (Shileiko, 1979).

At lower taxonomic levels too, the anatomy of the penial appendix provides valuable information. It is broadly separable into three regions; a relatively short basal portion which internally bears pilasters, and which may be everted (Figs 11C, 37A); a long, thin central stalk which is thick-walled and has only a very narrow lumen; and an elongate, apical sac which is thin walled with a large lumen. Shilieko (1979, fig. 4) recognised a total of five regions by including areas of differentiation at the top of the basal portion, and at the base of the central stalk. The function of the penial appendix is unknown, although Shileiko (1979) suggested it might act as a receptacle for autosperm prior to its injection into the spermatophore, and Forcart (1940) that it acted as a mechanical stimulator. It is present in all cerastines. The region of transition between the basal and central portions of the appendix, where the retractor muscle inserts, has proved to be of considerable taxonomic value in the cerastines, particularly at the generic level. In Arabian *Euryptyxis* the muscle inserts more-or-less directly at the junction, although it may expand and embrace the base of the central stalk just prior to attachment. In *Zebrinops* (Fig. 37D), and to a greater extent in *Cerastus* (Fig. 15A), the muscle actually encloses the stalk base, becoming attached at the top and forming an enclosed lumen; this trend is even more pronounced in the Ethiopian and Somali species of *Cerastus* and *Zebrinops* (Mordan, pers. obs.). The enclosure of the base of the central stalk is accompanied by the projection of the tip of the stalk into the basal lumen as an elongate papilla, which is particularly prominent in *Zebrinops* (Fig. 37D). The degree of contraction of the muscular sheath would partly determine the extent of protrusion of the papilla, and this may in turn be related to the state of relaxation of the individual specimen. Nevertheless, real differences in the length of the sheath, and of the papilla, do appear to exist between taxa.

The penis has a muscular sheath which is attached only at its top, and which in certain species appears always to be reflected to form a double-layered structure. There is a clearly demarked caecum which varies greatly in both size and shape between species, ranging from a short bulb in *Euryptyxis* to a long, so-called 'flagellum' in *Cerastus*. Whilst there are marked differences in both pilaster pattern and degree of differentiation of the caecal area between genera, within *Euryptyxis*, for example, pilaster pattern is fairly uniform: paired glandular pads embrace the epiphallar pore and extend downwards as pilasters which may bifurcate. Normally there is a further pair of glandular pads and associated pilasters opposite the pore. In two of the four species of *Euryptyxis* the glandular pads are divided latitudinally by a groove running round the penis below the level of the pore (Figs 24B, 27B), but in *E. candida* and *E. latireflexa* (Figs 21C, 31C) the groove appears to be absent. This groove is also well defined in *Zebrinops*, but in this genus no large glandular pads extend above it and the whole area of the caecum is dotted with small glandular areas (Fig. 37D).

The epiphallus itself has a relatively simple structure in *Euryptyxis* and *Zebrinops*, and appears externally as a thickened portion of the vas deferens with a series of transverse ridges or folds corresponding to a single internal row of pits which mould the spines of the spermatophore. The number of these pits does vary within species, but in the case of the four recognised Arabian species of *Euryptyxis* at least, there is no overlap in range between individual species (Table 5). An analysis of variance of the data shows highly significant between-species variation ($F = 168{\cdot}53$, d.f. 3,31. $p < 0{\cdot}001$). The African species *E. revoili* (24-25 pits) falls within the range of the Arabian *E. latireflexa* (17-28 pits), but the geographical distributions of these two species do not overlap. Moreover, their terminal genitalia differ in a number of other significant respects. Although most of the data in Table 5 were obtained from sympatric populations, where interspecific differences might be expected to be more pronounced, the limited evidence from allopatric populations of *E. fragosa* and *E. latireflexa* suggests this is not the case. Much larger epiphallar differences existed between syntopic *E. fragosa* and *E. candida* at Taizz, than between *latireflexa* and *labiosa* in Dhofar, but whereas the latter species pair differ in size quite markedly, the former are of very similar adult size and some alternative species-isolation mechanism such as genital or spermatophore incompatibility might need to be invoked.

The spermatophore of *Euryptyxis* is unknown except for a few broken fragments found in the spermatheca of *E. fragosa*. These suggest that the structure is similar to *Zebrinops*, but at least some of the spines have five points at their tip rather than two as in *Z. albata*. *Cerastus schweinfurthi* also has a single row of spines on the spermatophore. It is tempting to speculate on the possibility of the spermatophore structure acting as, or reinforcing, some form of species-isolation mechanism, but direct evidence is lacking, and the importance of inter-specific genital differences in mechanical isolation may well have been overestimated (Mayr, 1963). Nevertheless, such characters can be of considerable empirical value in taxonomy (Arnold, 1973, 1983), and although the epiphallus cannot be considered a part of the external genitalia, it does secrete the spermatophore and presumably would be subject to selection pressures similar to those acting on the external genital organs.

The Enidae exhibit a rather greater variety of terminal genital structures than do the cerastines. In particular, the penial appendix is lacking in a number of genera, and a diverticulum is often developed on the spermathecal stalk. Forcart (1940) based his separation or the Turkish Enidae into the two subfamilies Eninae and Chondrulinae on the presence or absence of the penial appendix, and on this basis both subfamilies are represented in northern Oman. The generic placement of the two northern Oman enids is based principally on the anatomy of the terminal genitalia.

Ecology

Extremely little is known of the ecology of the southern Arabian land snail fauna. In common with most desert pulmonates much of the year is spent in aestivation, with only limited periods of activity during the wet seasons. The main precipitation results from the south-west monsoon during July and August, but there may be other shorter periods of rainfall during the year. In general, cerastines aestivate in shaded situations on trees and rocks, normally some distance above ground level. *Mastus* and *Imparietula* are known to utilise similar sites, but they are also commonly found in considerable numbers in soil under rocks and ground litter such as palm fronds. Whilst most cerastine species are largely restricted to upland regions, *Imparietula* and *Mastus* also occupy synanthropic sites in plantations and near houses at lower elevations.

A consideration of population structure of *Euryptyxis* during aestivation suggests that in most species maturity is normally reached in two growing seasons (not necessarily annual), and that the adults subsequently live for a number of years. Only two size classes appear to be represented, and adults greatly outnumber the juveniles.

The importance of predation is uncertain, but many aestivating colonies of *Euryptyxis* in Dhofar showed evidence of some snails having been broken off, leaving the shell lip adhering to the substrate. The most likely predators are small mammals such as the spiny mouse *Acomys,* three species of which are recorded from Dhofar (Harrison, 1980), and the rat *(Rattus rattus)* which is now present in many areas. Rodents in particular are known to exert a significant effect on population densities of desert snails in the Negev (Yom-Tov, 1970).

Sympatry of closely related species is of considerable taxonomic interest as it can provide the only situations in which the species may interact. In the problematical genus *Euryptyxis* the syntopic occurrence of the following species pairs was recorded: *E. fragosa* and *E. candida* [Taizz, 1978-79]; and *E. latireflexa* and *E. labiosa* [Tawi Atair, 1977-78]. It also seems likely that *Cerastus schweinfurthi* and *C. scotti* co-occur at Jebel Harir (Connolly, 1941), but living material is lacking. From the limited information available, however, there was no real evidence for any form of character displacement in sympatric populations when compared with those from allopatric situations.

Summary and conclusions

A total of sixteen species of Enidae *sensu lato* are recognised in the present revision, from a list of thirty nominal species given by Connolly (1941); only one, *Cerastus albonotata* Verdcourt, has been newly described since that time. Whilst these figures appear to represent a synonymy ratio of 2:1, such a conclusion would be false, as almost the entire synonymy is accounted for within the single genus *Euryptyxis.*

The most significant taxonomic changes presented concern the generic repositioning of a number of taxa listed by Connolly under *Euryptyxis,* and in particular the placement of the northern Oman species into genera belonging to the essentially Palaearctic subfamilies Eninae and Chondrulinae. Within the Cerastinae, the existing generic units have been retained, but have now been defined in terms of anatomical as well as shell characters. In doing this it has been necessary to use additional corroborative data on closely related taxa from Somalia, Ethiopia and Socotra. In general there has been insufficient material to assess anatomical variation adequately. Indeed the anatomy of a large number of the taxa remains unknown. The greatest information was available for the commonest and most-widespread genus *Euryptyxis* and here in was demonstrated that species were better defined in terms of epiphallar rather than penial anatomy, suggesting that spermatophore morphology might play a role in species isolation.

Consistent, and I believe significant, anatomical differences have been shown to exist between the northern subfamilies Eninae and Chondrulinae (referred to here as the Enidae *sensu stricto),* and the southern Cerastinae. The former are uniquely defined by the possession of a clump of *culs-de-sac* on the hermaphrodite duct, whilst the latter show a number of specialisations of the pallial complex, apparently related to water conservation, as well as of the reproductive system. Moreover, there appear to be no synapomorphic characters to unite the two as sister groups in a cladistic sense. Formalization of these differences in nomenclature is, however, deferred until there is greater knowledge of the anatomy of related orthurethran families.

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References

Albers, J. C. 1860. *Die Heliceen nach naturlicher Verwandtschaft systematisch geordnet*. Second Edition. 359pp. Leipzig: Engelmann.

Ancey, C. F. 1906. Relevé des mollusques terrestres et fluviatiles de la Pénsule Arabique. *J. Conch. Paris* **53:** 257–271.

Arnold, E. N. 1973. Relationships of the Palaearctic lizards assigned to the genera *Lacerta, Algyroides and Psammodromus* (Reptilia:Lacertidae). *Bull. Br. Mus. nat. Hist.* (Zool). **25:** 291–366.

—— 1983. Osteology, genitalia and the relationships of *Acanthodactylus* (Reptilia:Lacertidae). *Bull. Br. Mus. nat. Hist.* (Zool.) **44:** 291–339.

Bayne, C. J. 1973. Physiology of the pulmonate reproductive tract: location of spermatozoa in isolated, self-fertilising succineid snails (with a discussion of pulmonate tract terminology). *Veliger* **16:** 169–175.

Beck, H. 1837. *Index Molluscorum*. 124pp. Hafniae.

Beck, K. 1912. Anatomie deutscher Buliminus-Arten. *Jena. Z. Naturw.* **48** (2): 187–262.

Bourguignat, M. J. R. 1857. Améneties malacologiques. *Revue Mag. Zool.* Ser. 2, **9:** 3–21.

—— 1876. *Species novissimae Molluscorum in Europaeo systemati delectae* . . . 80pp. Lutetiae.

—— 1882. *Mission G. Révoil au Pays Comalis. Mollusques Terrestres et Fruviatiles*. 108pp. Paris.

Bruguière, J. G. 1792. *Encyclopédie Méthodique, Histoire Naturelle des Vers*. **1** 757pp. Paris.

Cain, A. J. 1977. Variation in the spire index of some coiled gastropod shells, and its evolutionary significance. *Phil. Trans. R. Soc., B.* **27** (956): 377–428.

—— 1981. Possible ecological significance in shape of *Cerion* shells with age. *J. Conch. Lond.* **30:** 305–315.

—— 1982. On homology and convergence. *In* K. A. Joysey & A. E. Friday, *Problems of phylogenetic reconstruction. The Systematics Association Special Volume* **21:** 1–19.

—— 1983. Ecology and ecogenetics of terrestrial molluscan populations. *In:* K. M. Wilbur (Ed.), *The Mollusca* **6:** 597–647. Academic Press. London & New York.

Connolly, M. 1925. The non-marine Mollusca of Portugese East Africa. *Trans. R. Soc. S. Afr.* **12** (3): 105–220.

—— 1941. South Arabian non-marine Mollusca. *Expedition to south-west Arabia, 1937–8*. **1** (4): 17–42.

Dance, S. P. 1966. *Shell Collecting. An Illustrated History*. 344pp. Faber & Faber, London.

Dejean, Baron. 1821. *Catalogue de la collection des Coléoptères*. 136pp. Paris.

Delessert, B. 1841. *Recueil de coquilles décrites par Lamarck* . . . 40 Pls. Paris.

Dillwyn, L. W. 1817. *A descriptive catalogue of recent shells, arranged according to the Linnaean method; with particular attention to the synonymy*. 1092pp. London.

Férussac, J. B. L. A. de. 1821–22. *Tableau systématiques des animaux mollusques* 114pp. Paris.

—— 1827. *Bull. Sci. nat. Geol.* **8:** 85.

Férussac, J. B. L. A. de. & Deshayes, G. P. 1951. Histoire naturelle générale et particulière des Mollusques. . . . 2 Vols., Atlas. Paris.

Fischer-Piette, E. & Métivier, B. 1972. Sur quelques mollusques terrestres du sud-est de l'Arabie. *Bull. Mus. Hist. nat. Paris* 3e série. **93:** 1289–1310.

Forcart, L. 1940. Monographie der Türkischen Enidae (Moll., Pulm). *Verh. naturf. Ges. Basel* **51** (1): 106–364.

Forskal, P. 1775. *Descriptiones Animalium.* 140pp. Hauniae.

Gmelin, J. F. 1791. *Linnaeus, Sysema Naturae,* 13th Ed. **I** (6): 3021–3909. Lipsiae.

Gittenberger, E. 1967. Die Enidae (Gastropoda, Pulmonata) gesammelt von der Neiderländischen biologischen Expedition in die Türkei in 1959. *Zool. Meded. Leiden* **42** (13): 125–141.

Harrison, D. L. 1980. The mammals obtained in Dhofar by the 1977 Oman Flora and Fauna Survey. *Journal of Oman Studies, Special Report* **2:** 387–397.

Heller, J. 1971. Revision of the genus *Paramastus* Hesse (Enidae). *Arch. Molluskenk.* **101** (5–6): 263–273.

—— 1974. Systematics and distribution of the land snail *Pene* (Pulmonata: Enidae) in Israel. *Zool. J. Linn. Soc.* **54** (4): 257–276.

—— 1975. The taxonomy, distribution and faunal succession of *Buliminus* (Pulmonata: Enidae). *Zool. J. Linn. Soc.* **57** (1): 1–57.

Herrmannsen, A. N. 1847. *Indicis generum malacozoorum primordia . . .* **2:** 1–352. Casselis.

Hesse, P. 1933. Zur Anatomie und Systematik der Familie Enidae. *Archiv Naturgesch.* N.F. **2** (2): 145–224.

Hubendick, B. 1978. Systematics and comparative morphology of the Basommatophora. *In:* V. Fretter & J. F. Peake (Eds.), *Pulmonates* **2A:** 1–47.

Jousseaume, F. 1889. Espèces nouvelles des environs d'Aden suivies d'un apercu sur la faune malacologique de la Péninsule Arabique. *Bull. Soc. malac. Fr.* **6:** 345–362.

—— 1890. Espèces terrestres de Massaouah, de Perim et d'Aden. *Bull. Soc. malac. Fr.* **7:** 81–102.

—— 1894. Diagnose des coquilles de nouveaux mollusques. *Bull. Soc. philomath. Paris. 3rd Series* **6** (3): 98–104.

—— 1899. Description of coquilles nouvelles. *Naturaliste* 2nd. Series **13:** 8.

Kobelt, W. 1902. Die Familie Buliminidae. In *Systematisches Conchilien-Cabinet.* pp. 397–1051. Nurnberg.

Küster, H. C. & Pfeiffer, L. 1845–55. Die gattung *Bulimus.* In: *Systematisches Conchilien-Cabinet.* 395pp. Nurnberg.

Lamarck, J. P. B. A. de M. de 1822. *Histoire Naturelle des Animaux sans Vertèbres.* **6** (2) 232pp. Paris.

Lindholm, W. A. 1925. Beitrage zur Systematik und Nomenklatur der Familie Enidae (Buliminidae). *Arch. Molluskenk.* **57:** 23–41.

Martens, E. von, 1895. Neuen *Buliminus* aus Süd-Arabien. *Sber. Ges. naturf. Freunde Berl.* 1895 (6): 129–130.

Martens, E. von & Wiegmann, F. 1898. Land- und Süsswasser-Mollusken der Seychellen. *Mitt. zool. Samml. Mus. Naturk. Berl.* **1** (1): 1–94.

Martini, F. H. W. & Chemnitz, J. H. 1786. *Neues systematisches Conchylien-Cabinet.* 9 345pp., 33 pls. Nuremberg.

Mayr, E. 1963. *Animal species and evolution* 797pp. Cambridge, Mass.

Melvill, J. C. 1894. Descriptions of two new species of terrestrial Mollusca from the Hadramaut District, South Arabia. *Proc. malac. Soc. Lond.,* **1:** 224–225.

Mermod, G. 1951. Les types de la collection Lamarck au Muséum de Genève. Mollusques vivants II. *Revue suisse Zool.,* **58** (40): 693–753.

Mol. J.-J. van, & Coppois, G. 1980. Mollusques, Enidae. *Revue zool. afr.* **94:** 15–60.

Mordan, P. B. 1980*a*. Molluscs of Saudi Arabia: land molluscs. *Fauna of Saudi Arabia* **2:** 359–367.

—— 1980*b*. Land Mollusca of Dhofar. *Journal of Oman Studies* Special Report. **2:** 103–111.

—— 1984. Taxonomy and biogeography of southern Arabian Enidae (sensu lato) (Pulmonata:Pupillacea). *In:* A. Solem & A. C. van Bruggen (Eds) *World-wide Snails: Biogeographical studies on non-marine Mollusca.* 289pp. Leiden.

Müller, O. F. 1774. *Vermium terrestrium et fluviatilum . . .* Vol. II, Havniae & Lipsiae.

Paladilhe, A. 1872. Voyage de Mrs. Antinori, Beccari et Issel dans la Mer Rouge et la pays des Bogos. Mollusques. II. Description de quelques espèces nouvelles des environs d'Aden. *Annali Mus. civ. Stor. nat. Genova* **3:** 12–26.

Pallary, P. 1925. Note on some terrestrial Mollusca from the hinterland of Makalla. *In:* O. H. Little (Ed.) *The geography and geology of Makalla (South Arabia).* 223–234. Cairo.

—— 1928. Mollusques continentaux du Sud de l'Arabie collectés en 1926 par M. Lees. *Proc. malac. Soc. Lond.* **18:** 39–42.

Peake, J. F. 1978. Distribution and ecology of the Stylommatophora. *In:* V. Fretter & J. F. Peake (Eds) *Pulmonates* **2A:** 429–526.

Pfeiffer, L. 1842. *Symbolae ad Historiam Helicorum.* II. 1–147. Cassel.

—— 1858. Diagnosen neuer Schnecken-Arten. *Malakozool. Bl.* **5:** 238–240.

Pilsbry, H. A. 1897. New Lower Californian Bulimuli. *Nautilus* **10:** 102–3.

—— 1897–98. *Manual of Conchology*. Second series: Pulmonata. Vol XI. 339pp. Philadelphia.

Pilsbry, H. A. & Cooke, C. M. 1914. *Manual of Conchology*. Second series: Pulmonata. Vol XXII. 428pp. Philadelphia: Academy of Natural Sciences.

Pollard, E. 1975. Differences in shell thickness in adult *Helix pomatia* from a number of localities in southern England. *Oecologia* **21:** 85–92.

Récluz, C. A. 1843*a*. Description de coquilles rapportées par M. Jehenne. *Revue zool.* **1843** (1): 2–5.

—— 1843*b*. *Magasin Zool. Paris* Series 2, Classe 5, 5: pls. 75–76. Paris.

Reeve, L. A. 1849. Monograph of the genus *Bulimus. In Conchologica Iconica* 5. 89pls. London.

Rossmassler, E. A. 1835–1920. *Iconographie der Land- & Süsswasser Mollusken* ... Series 1 and 2. Completed P. Hesse. Dresden, Leipzig, & Berlin.

Selander, R. K. & Hudson, R. O. 1976. Animal population structure under close inbreeding: the land snail *Rumina* in southern France. *Am. Nat.* **110:** 695–718.

Seshaiya, R. V. 1932. Anatomy of *Rachisellus punctatus* (Anton). *Annamalai University Journal* **1** (1): 72–90.

Shachak, M., Orr, Y. & Steinburger, Y. 1975. Field observations on the natural history of *Sphincterochila (S.) zonata* (Bourguignat, 1853). *Argamon* **5** (1–4): 20–46.

Shileiko, A. A. 1979. The system of the order Geophilla (= Helicida) (Gastropoda Pulmonata). *Proceedings of the Zoological Institute, Academy of sciences of the USSR.* **80:** 44–69.

Smith, E. A. 1894. On a small collection of land and freshwater shells from Oman, Arabia. *Proc. malac. Soc. Lond.* **4** (4): 141–142.

—— 1903. Land and freshwater shells of Socotra and Abdel-Kuri. *Liverpool Museum Reports, Socotra Expedition*. pp. 111–158.

Smythe, K. & Gallagher, M. 1977. Land and freshwater Mollusca. *Journal of Oman Studies* Special Report. **1:** 219–225.

Solem, A. 1962. Notes on, and descriptions of New Hebridean land snails. *Bull. Br. Mus. nat. Hist.* (Zool.) **9** (5): 217–247.

—— 1964. *Amimopina*, an Australian enid land snail. *Veliger* **6** (3): 115–120.

—— 1973. Convergence in pulmonate radulae. *Veliger* **15** (3): 165–171.

—— 1978. Classification of the land Mollusca. *In:* V. Fretter & J. F. Peake (Eds), *Pulmonates* **2A:** 49–97. London.

—— 1979. Biogeographic significance of land snails, Paleozoic to Recent. *In:* J. Gray & A. J. Bucot (Eds) *Historical biogeography, plate tectonics and the changing environment*. pp. 277–287. Oregon.

Steenberg, C. M. 1914. Anatomie des Clausilies Danoises. I. Les organes génitaux. *Mindeskrift for Japetus Steenstrup* **29:** 1–44.

—— 1925. *Etudes sur l'Anatomie et la Systématique des Maillots*. 211pp., 34 pls. Copenhagen.

—— 1929. Recherches sur l'anatomie et la place systématique du genre *Agardhia* Gude (Gastropoda Pulmonata, fam. Pupillidae *s. lat.*). *Vidensk. Meddr. dansk naturh. Foren.* **88:** 15–29.

Sykes, E. R. 1902. Description of *Cerastus dinshawi* n. sp. from Aden with a note on *Otopoma*. *Proc. malac. Soc. Lond.* **5:** 338–9.

Taha, M. F., Harb, S. A., Nagib, M. K. & Tantawi, A. H. 1981. The climate of the Near East. *In:* K. Ttakahashi & H. Arakawa (Eds), *World survey of climatology*. 333pp. Amsterdam.

Tillier, S. 1981. Clines, convergence and character displacement in New Caledonian diplommatinids (Land Prosobranchs). *Malacologia* **21** (1/2): 177–208.

—— 1982. Structures respiratoires et excrétrices des limaces (Gastropoda:Pulmonata:Stylommatophora). *Bull. Soc. Zool. Fr.*, **108:** 9–19.

Verdcourt, B. 1966. Notes on the genus *Conulinus* MARTENS (Enidae). *Arch. Molluskenk.* **95** (5/6): 279–286.

—— 1970. The genus *Cerastua* Strand (Mollusca-Enidae) in the Congo Republic, Burundi and Rwanda. *Revue zool. afr.* **82** (1–2): 14–34.

—— 1974. Notes on a small collection of non-marine Mollusca from Yemen. *J. Conch. Paris* **111:** 3–8.

Visser, M. H. C. 1977. The morphology and significance of the spermoviduct and prostate in the evolution of the reproductive system of Pulmonata. *Zoologica Scr.* **6:** 43–54.

Watson, H. 1920. The affinities of *Pyramidula, Acanthinula,* and *Vallonia*. *Proc. malac. Soc. Lond.* **14** (1): 6–30.

Wenz, W. 1923. Gastropoda extramarina tertiaria II, Pulmonata II. *In:* J. F. Pompeckj, *Fossilium Catalogus*. p. 885–1734. Junk: Berlin.

Westerlund, C. A. 1887. *Fauna der in der Paläartischen Region Lebenden Binnenconchylien.* **1** (3). 183pp. Lund.

Wiegmann, F. 1901. Binnen-Mollusken aus Westchina und Centralasien. II. Die Buliminiden. *Ezheg. zool. Muz.* **6:** 221–298.

Woodruff, D. S. 1978. Evolution and adaptive radiation of *Cerion:* a remarkably diverse group of West Indian land snails. *Malacologia* **17:** 223–239.

Yom-Tov, Y. 1970. The effects of predation on population densities of some desert snails. *Ecology.* **51:** 907–911.

Zilch, A. 1951. Ergebnisse zoologisch-geologischer Sammelreissen H. Kaltenbach's in NO-Afrika, **5:** Familie Enidae. *Arch. Molluskenk.* **80:** 33–46.

—— 1959. Gastropoda 2. Euthyneura. *In:* O. H. Schindewolf (Ed.), *Handbuch der Paläozoologie.* pp 1–200. Berlin. PA

Abbreviations used in figures

A	anus
AC	albumen chamber
AD	albumen duct
AG	albumen gland
AO	aorta
AP	appendicular papilla
AR	appendicular retractor
AT	atrium
ATR	atrial retractor muscle
AU	auricle
C	caecum
CR	crop
E	epiphallus
EC	epiphallar caecum
EF	epiphallar flagellum
EP	epiphallar pore
EPT	epiphallar pit
I	intestine
GO	genital orifice
HD	hermaphrodite duct
HDC	hermaphrodite duct culs-de-sac
HG	hermaphrodite gland
K	kidney
MC	mantle collar
MG	mantle gland
MS	muscle sheath
O	oviduct
OE	oesophagus
P	penis
PA	penial appendix
PI	pilaster
PP	penis papilla
PR	penis retractor
PN	pneumostome
PV	pulmonary vein
R	rectum
RNF	renal fold
RTF	rectal fold
RO	renal orifice
S	spermatheca
SD	spermathecal diverticulum
SG	salivary gland
SO	spermoviduct
ST	stomach
SV	seminal vesicle
T	talon
V	vagina
VD	vas deferens
VE	ventricle

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British Museum (Natural History)

The littorinid molluscs of mangrove forests in the Indo-Pacific region

D. G. Reid

Periwinkles (family Littorinidae) are amongst the most intensively studied of marine gastropods, because of their worldwide distribution and abundance in the intertidal environment. This monograph is a comprehensive account of the taxonomy, biology and biogeography of the *'Littorina scabra'* species complex, a hitherto poorly-known group of littorinids ubiquitous in mangrove habitats throughout the Indo-Pacific region. Twenty species are recognized, where most previous authors have distinguished only three. Detailed accounts of the anatomy of each species are given, with particular attention to the reproductive system, by which the species can be reliably distinguished. A key to shells is provided, and 100 figures and plates illustrate the range of shell variation, anatomical characters and geographical distribution of each species.

Drawing on comparisons with ten littorinid genera, evolutionary trends in the morphology of male and female reproductive tracts, sperm nurse cells, egg capsules, reproductive modes and radulae are discussed. These features are assessed as taxonomic characters, and the large literature on the morphology of the family is reviewed. Cladistic analysis of anatomical characters supports a reclassification of the Littorinidae, including placement of the *'scabra'* group in the genus *Littoraria*.

In addition to molluscan systematists, this monograph should be of interest to marine biogeographers and ecologists working in the mangrove environment. In recent years much ecological and genetical research has been stimulated by the discovery of sibling species of *Littorina* in Europe. The *Littoraria* species have a similar potential in the Indo-Pacific, where up to ten species may occur sympatrically. Several of the species are polymorphic for shell colour and have already been used as material for the study of mechanisms of natural selection.
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R. W. Sims

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Revision of the western African earthworm genus *Millsonia* (Octochaetidae: Oligochaeta) with notes on two new species of the genus *Agastrodrilus* (Octochaetidae) from Ghana

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Synopsis

The western African earthworm genus *Millsonia* Beddard, 1894 is revised. A table of diagnostic characters, descriptions and figures are provided for 27 species regarded as valid, of which 14 are described as new. Three taxa previously associated with the genus are excluded: *meridionalis* Omodeo, 1972 is transferred to *Dichogaster* Beddard, 1888 s.l. and *schlegeli* Horst, 1884 to *Benhamia* Michaelsen, 1889; *Dichogaster insignis* Michaelsen, 1922 is regarded as a species *incertae sedis*. Notes are also provided on the allied genus *Agastrodrilus* Omodeo & Vaillaud, 1967 with descriptions of two new species.

Introduction

Earthworms of the genus *Millsonia* inhabit the soils of the wet savannah and forest regions of western Africa from the Ivory Coast eastwards to Nigeria. Although the ranges partly overlap, the genus is replaced in the soils of the drier savannahs to the north and west by the allied *Benhamia;* both, however, are sympatric with their more widely distributed mutual relative, *Dichogaster*. Until comparatively recently only a few species of *Millsonia* were recognized, but following surveys in the Ivory Coast (Omodeo, 1958) and especially Ghana, the situation has changed radically. Collections were made in connection with the ecological surveys carried out by the laboratory at Lamto, Ivory Coast, while Miss M. Tazelaar collected earthworms around Kumasi, Ghana (Sims, 1965*a*). Even more recently, Professor J.J. Niles made further collections in the Kumasi region, then, in 1966, Dr J.D. Plisko Winkworth visited Ghana and sampled earthworm populations throughout the country. These latter series were eventually presented to the British Museum (Natural History) where they were found to contain so many new species of *Millsonia* that it became necessary to undertake a special study of the genus. The results of this investigation form the subject of the present report with the genus here recognized as comprising some 27 species of which 14 are described as new to science. Additionally, it emerges that the species occur in a wide range of habitats, spreading from the forests and wet savannahs into cultivation, i.e. from

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plantations to village fields, gardens and even to the Botanic Gardens at Aburi,Ghana. Two new species of the morphologically similar genus *Agastrodrilus* were also collected and are described later in the report.

Morphology

Size. Most species of *Millsonia* are large, a few being over 500 mm in length, and several having more than 500 body segments. However, some have small-sized individuals seldom exceeding 100 mm in length with fewer than 200 body segments.

Setae. Usually small and uniform in size and shape, not always to be seen anteriorly in mature individuals. (The ventral setae in the anterior region are considerably enlarged in species of the genus *Agastrodilus*.)

Dorsal pores. The first dorsal pore is variably located in a pre-clitellar furrow according to species. Its situation seems *not* to be correlated with the thickening, i.e. the muscularization, of the anterior septa (see below) that reflects the burrowing prowess of a species.

Clitellum. Chiefly saddle-shaped; present over at least segments *xiv–xvii*, commonly extending *xiii–xix*. The genital field, which is enclosed between the ventral borders of the clitellum, is highly variable in appearance, being characteristically developed for each species. The clitellum is often well developed in immature individuals (gonads poorly developed, seminal vesicles absent).

Male terminalia. Species of the genus form two assemblages according to the arrangement of the male and prostatic pores. Over half of the species have an acanthodriline arrangement (male pores paired *xviii*, prostatic pores paired *xvii* and *xix*), while the remainder have a microscolecine reduction with the male and prostatic pores paired only on segment *xvii*. The male pores are sometimes carried on porophores but mostly they are superficial and commonly discharge into paired genital pouches or perhaps a single median pouch. (The pouches are everted during copulation, and often during relaxing, killing and fixing when preserving specimens).

Spermathecal pores. In species with an acanthodriline arrangement of the male terminalia, the spermathecae occur in two segments, *vii* and *ix*, and consequently open into furrows 7/8/9. Among other species that have a microscolecine reduction of the male terminalia, there is only a single pair of spermathecae. Apart from two exceptions, *hemina* and *oracapensis*, that have the spermathecae opening into 7/8, the spermathecae open into furrow 8/9. The spermathecal pores are located the same distance apart as the male pores. The furrows into which they open are appropriately modified whenever the genital field is specialized, since the pores of the opposing systems of concopulants are closely applied during sperm transfer. Whenever the male pores open into deep, pit-like, genital pouches that are everted during copulation, the latter are accommodated by invaginations (*vestibula*, i.e. 'vestibules') that develop in the furrow in the vicinity of each spermathecal pore. The spermathecal pore is rarely single (median ventral only in *ditheca*), but a single mid-ventral vestibule may develop with maturity (as in *nigra*) although the pores within are paired (Sims, 1965*b*).

Female pores. Located on segment *xiv*, the female pores are usually paired near setal lines *a* or *b*, sometimes within *aa*; the pore is rarely single (mid-ventral in *ditheca* and *nilesi*).

Genital papillae. Papillate and transverse, glandular pads are common ventrally in the clitellar region and on nearby segments in fully adult individuals of most species. The papillae are mostly large with a single pair occurring on each segment, but occasionally they are small and irregularly scattered in discrete areas on the segments. Although papillae are usually arranged in discrete species-distinct patterns, there is considerable intraspecific variation in their development so that the full specific complement is seldom realized.

Septa. Interspecific differences in the thickening (muscularization) of the anterior septa are widespread, but even so they are not employed taxonomically. They do, however, signify that the included species have highly variably burrowing abilities and divergent life styles.

Gizzards. Two simple gizzards are present, and they are invariably separate. The anterior gizzard is in segment *v* and separated by septum 5/6 from the posterior gizzard in *vi*. They are usually uniform, but occasionally one is reduced being either smaller or less muscular, or exceptionally, vestigial as in *anomala*. (Both gizzards are reduced in *Agastrodrilus*.)

Calciferous glands. These are stalked, lamellate structures, paired dorso-laterally on the oesophagus in segments *xv, xvi, xvii*. Occasionally the anterior pair is reduced, e.g. *anomala, brevicingulata, centralis*.

Intestine. The last oesophageal segment is clearly *xvii* (i.e. the location of the posterior pair of (oesophageal) calciferous glands), in segment *xviii* the gut is transitional in structure since it begins to dilate while becoming thinner-walled so that in *xix* it forms the anterior end of the intestine. Apart from young juveniles, paired segmental caeca occur in 1 to 36 segments of the anterior intestine with the foremost pair located between segments *xxiv* and *xxx*. The number of caecal pairs is more or less constant for each species, but where there is a long series of caeca, the posterior pairs become progressively smaller until the posteriormost may be difficult to detect. The caeca are morphologically digitate and never saccular, thus the condition of the anterior intestine differs from the pouch-like shape present in contracted specimens of many western African species of *Dichogaster*.

Testes. Holandric, within paired testis sacs in segments *x* and *xi*.

Prostates. These may be paired in segments *xvii* and *xix* (acanthodriline arrangement) or in segment *xvii* only (miscroscolecine reduction). They may form a simple 'U' and be confined to a single segment of become highly convoluted and encroach into nearby segments. Ectally each gland becomes muscular to form a slender duct that leads to the exterior; generally the length of the duct varies according to the species.

Spermathecae. Invariably located in segments *viii* and/or *ix*. Spermathecae (usually paired) occur in both segments in species with an acanthodriline arrangement of the male terminalia but in species with a microscolecine reduction of the male terminalia, there is a single pair in only one segment. The species *ditheca* is exceptional in having only a single, unpaired, median ventral spermatheca in each of segments *viii* and *ix* (see above *Spermathecal pores*). About half of the species have simple, adiverticulate spermathecae. The spermathecae of most other species have one or two diverticula, mostly arising from the duct but occasionally on the ampulla; the diverticula are usually unilocular and only rarely multilocular.

Nephridia. Closed exonephric meronephridia are present on the parietes throughout most of the body; they are usually reduced or absent from the anterior, mainly pre-testicular, segments where they may occur on the septa. In the oesophageal segments the meronephrida tend to be diffuse, but in the intestinal segments they become more saccular and discrete with perhaps 10 to 12 forming a row along the equator of a segment, with each discharging directly to the exterior. Many species have an additional pair of open holonephridia in each intestinal segment. Each holonephridium consists of a long duct leading peripherally over the parietes to the dorsum from a ventral nephrostome opening in the preceding segment; the duct is looped and becomes convoluted before discharging to the exterior on the equator of the segment about setal distance *aa* from the mid-dorsal line. Terminal vesicle or bladder not seen, presumably absent from each holonephridium. The coiled portion of the holonephridial duct has subsidiary convolutions that possibly function as closed meronephridia. An additional specialization was reported in *M. anomala* by Omodeo

(1955); here the holonephridial ducts of each side communicate with a (paired) longitudinal canal on the parietes on both sides of the ventral nerve cord.

The discrete meronephric condition occurs in most species with numerous intestinal caeca (over ten pairs), whereas the combined meronephric and holonephric condition is present in the majority of species with fewer than ten pairs of intestinal caeca. This correlation between the presence of numerous pairs of intestinal caeca and the absence of holonephridia makes the causal factors seemingly physiological, i.e. species adaptations to their habitat niches. Among earthworms of the family Megascolecidae, the structure of the excretory system appears to be highly plastic with frequent partial or complete replacement of holonephridia by meronephridia, even among congeneric species. The occurrence of meronephridia does not therefore appear to represent a highly significant phylogenetic event, but instead a common phenomenon that may occur even within a minor radiation whenever it is advantageous for emergent groups to adjust to changing conditions or to exploit new niches. The incidence of both nephridial conditions among species of the genus *Millsonia* thus parallels comparable situations in the family Megascolecidae and, in doing so, casts doubts on the validity of the family Octochaetidae that is currently delineated from the family Acanthodrilidae with only holonephridia by having only meronephridia.

Taxonomy

The megascolecoid genus *Millsonia* was erected by Beddard (1894) for two non-perichaetine, meronephric species lacking penial setae but with paired male and prostatic pores combined on segment *xvii*, two gizzards, three pairs of calciferous glands and paired intestinal caeca. At that time, megascolecoid earthworms with a lumbricine arrangement of the setae and spermathecae in the pre-testicular segments were divided into the family Cryptodrilidae (male and prostatic pores paired on segment *xvii* or *xviii*) and the Acanthodrilidae (male pores paired on segment *xviii* and the prostatic pores paired on segments *xvii* and *xix*). Thus *Millsonia* was originally assigned to the family Cryptodrilidae to join, among others, its ally *Dichogaster* Beddard, 1888 (type species *D. damonis* Beddard, 1888 from Fiji having male pores on *xvii* with prostatic pores and further prostatic pores on *xviii* and *xix* but internally lacking intestinal caeca). When Michaelsen produced his monograph (1900), he considered the location and arrangement of the male terminalia to be relatively unimportant systematically and instead gave greater weighting to internal characters. Thus he united all of the meronephridial species of the Cryptodrilidae previously accommodated in *Dichogaster*, *Millsonia* and *Balanta* (the last was a related monotypic genus separated by Michaelsen in 1898 for a species with combined, paired male and prostatic pores on segment *xix*). Furthermore, they were placed with species of the genus *Benhamia* previously assigned to the family Acanthodrilidae to form a vast, heterogenous genus, *Dichogaster*, that accommodated all species with two gizzards and three pairs of calciferous glands. One result was that three species with an acanthodriline arrangement of the male terminalia and possessing intestinal caeca, *inermis* Michaelsen, *caecifera* Benham and *heteronephra* Michaelsen (all previously assigned to the genus *Benhamia*), were first brought together with *nigra* Beddard, the type species of *Millsonia* that has a microscolecine arrangement of the male terminalia (i.e. male and prostatic pores paired on segment *xvii* only).

During the next few decades, many new species were described in the genus *Dichogaster* to form what was clearly an heterogenous assemblage containing nearly two hundred nominal species. Eventually, Omodeo (1955) divided *Dichogaster s.l.* into six genera by separating the species on the number and location of the calciferous glands together with the occurrence of penial setae and intestinal caeca. The genus *Millsonia* was resurrected for the species without penial setae but, among other characters, possessing intestinal caeca. Subsequently, small-bodied species similar to *Millsonia*, but with enlarged ventral setae and rudimentary gizzards, were separated in the genus *Agastrodrilus* by Omodeo and Vaillaud, 1967 (see p. 309). This group of genera is now assigned to the family Octochaetidae *sensu* Gates (1959).

Genus ***MILLSONIA*** Beddard, 1894

Millsonia Beddard, 1894: 380; Beddard, 1895: 479; Omodeo, 1955: 218; Omodeo, 1958: 22 & 59.
Dichogaster (part): Michaelsen, 1900: 334; Stephenson, 1930: 851.

TYPE SPECIES. *Millsonia nigra* Beddard, 1894 (Omodeo, 1955, by subsequent designation).

DIAGNOSIS. Octochaetidae lacking penial setae with two simple, well-developed gizzards, the anterior gizzard in segment *v* and the posterior gizzard in *vi*; stalked, lamellate, calciferous glands paired on the oesophagus in segments *xv*, *xvi*, *xvii* (the anterior pair occasionally reduced); paired digitate caeca present in at least one, usually several adjacent segments, of the anterior region of the intestine; typhlosole present; setal couples *ab* and *cd* similar in size, small.

DISTRIBUTION. Ivory Coast, Ghana, Togo, Benin and Nigeria.

REMARKS. The genus is restricted to contain only species with two large, simple gizzards (never fused or partly fused gizzards) and lacking penial setae; thus species such as *schlegeli* Horst, 1884 and *meridionalis* Omodeo, 1973 with penial setae and fused gizzards are excluded. Examination of the types of *schlegeli* in the Rijksmuseum van Natuurlijke Historie, Leiden, reveals that Horst miscounted the segments and the species should be assigned to the genus *Benhamia* Michaelsen, 1889 (*sensu* Omodeo, 1955); this is clearly a taxon requiring a separate study (Michaelsen, 1914*a*). While *meridionalis* is seemingly a species of *Dichogaster* Beddard, 1888 (*sensu* Omodeo, 1955), a genus in which the anterior region of the intestine is commonly saccular in each segment (in contracted specimens this condition gives the appearance of the intestine being caecate).

On the other hand, the identity of *Dichogaster insignis* Michaelsen, 1922, known only from a single subadult collected at Juring on the Sulima River in eastern Sierra Leone, is problematic. Unlike *meridionalis* and *schlegeli*, this species from Juring possesses separate gizzards in *v* and *vi* and lacks penial setae, but intestinal caeca were not recorded by Michaelsen. (Examination of the unique holotype in the Rijksmuseum van Natuurlijke Historie, Leiden, does not resolve the question of the occurrence of intestinal caeca since the fore-gut has been removed and only the oesophageal portion has been separately retained in an included vial.) Unfortunately, comparisons with other species are made different because of the immaturity of the individual, with the clitellum, spermathecae and prostates being only poorly developed. Omodeo (1958: 59) assigned *insignis* to the genus *Millsonia* on the characters already noted, and also on the absence of diverticula from the spermathecae, a condition rarely encountered among western African octochaetids outside of the genus *Millsonia*. Examination during this current investigation of the holotype revealed additionally the absence of holonephridia, the occurrence of the female pores in setal line *a* and the lack of papillae and other external specializations; thus *insignis* would appear to resemble *M. centralis* from Central Ghana, a species with 14 pairs of intestinal caeca. However, to unite these two taxa would imply that Michaelsen either omitted to record or overlooked the presence of numerous intestinal caeca, clearly unacceptable requirements. In these circumstances, I propose to regard the taxon *Dichogaster insignis* Michaelsen, 1922 as a species *incertae sedis;* hopefully the acquisition of additional material from the type locality will, in time, help elucidate the problem of its generic identity. In any case, support for this decision is provided by distributional evidence as species of *Millsonia* have not been reported from Sierra Leone nor from the adjacent state of Liberia, the most westerly recorded so far coming from the Ivory Coast.

The comparative characters of the valid species currently included in the genus *Millsonia* are listed in Table 1.

Millsonia anomala Omodeo, 1955

(Figs 9D & 10D)

Millsonia anomala Omodeo, 1955: 219; Omodeo, 1958: 59; Sims, 1965*a*: 299.

DIAGNOSIS. Spermathecal pores paired in furrows 7/8/9 in setal lines *bb*; male pores paired *xviii*, prostatic pores paired *xvii* and *xix*; female pores paired near *a* immediately within *aa*; small closely paired papillae present $\frac{2}{3}$*viii* and in furrows 13/14 and 14/15, single transverse pads present mid-ventrally *xxi–xxv*; nine pairs of intestinal caeca *xxvi–xxxiv*; holo- and meronephric.

Table 1 Distinguishing characters of species of the genus *Millsonia*

Male pores segment no.	Spermathecal Pores		Female pores setal line	1st dorsal pore furrow	Intestinal caeca no. pairs	Species	Notes
	Furrow(s)	Setal line					
Meronephridia only present (holonephridia absent)							
xvii	8/9	across *cd*	distance *ab* below *a*	8/9	**1**	*sokodeana*	
xvii	8/9	across *ab* within vestibulum	ventral, $\frac{1}{3}$ *aa* apart	4/5	**16**	*ashantiensis*	
xvii	8/9	*c*	*a*	4/5	**32**	*mima*	copulatory 'pouch' and spermathecal vestibulum absent
xvii	8/9	across *ab*(imm.) within vestibulum (adults)	distance *ab* below *a*	5/6	**32 (25–36)**	*nigra*	copulatory 'pouch' and spermathecal vestibulum present
xviii	7/8/9	*b*	ventral $\frac{1}{2}$ *aa* apart	10/11	**(3)4(5)**	*pumilia*	
xviii	7/8/9	*b*	distance *ab* below *a*	7/8	**5—6**	*riparia*	
xviii	7/8/9	across *ab*	mid-ventral (single)	5/6	**14(13—17)**	*nilesi*	
xviii	7/8/9	across *ab*	*a*	11/12	**14—16**	*pulvillaris*	external transverse pads papillose;anterior gizzard small
xviii	7/8/9	across *ab*	*a*	12/13	**13–16**	*guttata*	external transverse pads without papillae; gizzards of equal size

xviii	7/8/9	*a*	*a*	5/6	**14**	*centralis*	anterior calciferous glands (*xv*), reduced in size
xviii	7/8/9	*b*	distance $\frac{1}{2}$ *ab* below *a*	12/13	**(11–)14**	*inermis*	external transverse pads absent; gizzards of equal size
xviii	7/8/9	*a*	*a*	4/5	**24**	*caecifera*	
Holonephridia and meronephridia present							
xvii	7/8	*b*	within *ab*	6/7	**1**	*oracapensis*	body length + 100 mm
xvii	7/8	*b*	within *ab*	8/9	**2**	*hemina*	body length – 100 mm
xvii	8/9	*b*	distance *ab* below *a*	8/9	**2**	*nota*	
xvii	8/9	*b*	within *ab*	9/10	**4–5**	*hortensis*	
xvii	8/9	across *ab*	distance 2*ab* below *a*	9/10	**7**	*jadwigae*	
xvii	8/9	*a*	distance $\frac{1}{2}$ *ab* below *a*	11/12	**8**	*moderata*	
xvii	8/9	across *ab*	distance $1\frac{1}{2}$ *ab* below *a*	10/11	**9**	*cruciventris*	
xvii	8/9	across *ab*	ventral $\frac{1}{3}$ *aa* apart	10/11	**6–12**	*artesetosa*	setae ventral but approximately equidistance apart
xviii	7/8/9	*b*	within *ab*	7/8	**1(2)**	*brevicingulata*	
xviii	7/8/9	above *d*	distance *ab* below *a*	11/12	**6–9**	*heteronephra*	
xviii	7/8/9	*b*	ventral $\frac{1}{2}$ *aa* apart	6/7	**7**	*omodeoi*	spermathecal pores in furrows
xviii	7/8/9	across *ab*	ventral $\frac{1}{2}$ *aa* apart	10/11	**7–8**	*ghanensis*	spermathecal pores located anteriorly to the furrows
xviii	7/8/9	single median	single median	11/12	**8**	*ditheca*	
xviii	7/8/9	*b*	distance $\frac{1}{2}$ ab below *a*	5/6	**9**	*anomala*	anterior gizzard reduced in size
xviii	7/8/9	across *ab*	ventral closely paired	5/6	**19**	*lamtoiana*	

DESCRIPTION. *External characters.* Length 110–124 mm, diameter 5–6 mm. Segments 180–249, multiannulate. First dorsal pore 5/6. Citellum ($\frac{2}{3}$ *xiii*) *xiv–xix*, saddle-shaped extending ventrally to within setal lines *bc*. Male pores paired *xviii* discharging into paired seminal grooves joining the (paired) prostatic pores in *xvii* and *xix* where they are located between setal lines *ab*. Female pores paired slightly within setal lines *aa*. Spermathecal pores paired in furrows 7/8/9 in setal line *b*, the anterior pair being larger. Papillae closely paired on the posterior surface of the mid-ventrum of *viii* and by the mid-ventral line in furrows 13/14/15; a swollen transverse pad occurs between setal lines *aa* on each of segments *xxi–xxv*, the more posterior pads being less well defined.

Setae uniform, small, closely paired, ventral; post-clitellar formula $aa:ab:bc:cd =$ 14: 1·2 : 9 1 where $dd =$ three-quarters of the body circumference.

Internal characters First septum 4/5, septa 5/6/7 greatly thickened, septa 7/8/9/10 less so. The anterior gizzard is weakly developed, being little more than a slight thickening of the oesophageal wall, whereas the posterior gizzard is strongly muscularized; the anterior pair of calciferous glands is often reduced in size. Intestinal caeca, nine pairs, present *xxvi–xxxiv*. Prostates paired *xvii* and *xix*, tightly convoluted each with a slender muscular ectal duct. Spermathecae paired *viii* and *ix*, adiverticulate, the duct and ampulla of each are approximately the same length. Nephridia: meronephridia occur throughout the body, a pair of holonephridia are additionally present in each intestinal segment where their ducts unite with paired longitundinal canals lying one on each side of the ventral nerve cord.

TYPE LOCALITY. Gagnoa, southern Ivory Coast.

RECORDS. 4C Gagnoa (6°04′N, 5°55′W), southern Ivory Coast; Nov. 1954 (syntypes of *Millsonia anomala)*, (see *Remarks* below).

DISTRIBUTION. Southern Ivory Coast.

REMARKS. The description and the text-figure are based on Omodeo (1955). See also the *Remarks* in the account of the morphologically similar species *M. omodeoi.*

Lavelle (1971) recorded that *M. anomala* constitutes a major part of the oligochaete fauna in the low-lying, wet areas of the Lamto savannah of the Ivory Coast where breeding occurs twice a year at the end of the rainy seasons. (For further ecological information see also: Lavelle, Douhalei & Sow, 1974; Lavelle & Meyer, 1976.)

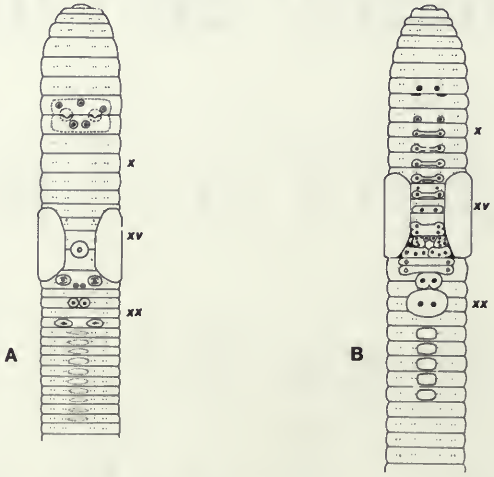

Fig. 1 *Millsonia* spp. with spermathecal pores in furrow 7/8; anterior region, ventral view (not to scale). (A)*oracapensis*; (B)*hemina.*

Millsonia artesetosa sp. nov.

(Figs 5F & 6F)

DIAGNOSIS. Spermathecal pores paired in furrow 8/9 in setal line *b*; combined male and prostatic pores paired on segment *xvii*; female pores paired $\frac{1}{3}$ *aa* apart within setal lines *aa* slightly anteriorly to the setal ring; papillae numerous, randomly arranged around the spermathecal and male pores, mid-ventral papillose pads may be present in furrows 13/14–15/16; setae widely paired approaching equidistance apart, ventral; intestinal caeca variable in number, six to twelve pairs beginning *xxix*, i.e. *xxix–xxxiv*, *xxxvii*, *xl*; holo- and meronephric.

DESCRIPTION. *External characters.* Length (aclitellate specimens 60–198 mm) clitellate specimens 186, 210 mm; diameter 5–8 mm. Segments 312–340, triannulate commonly with further subdivisions, especially anteriorly where external determination of the segments is often difficult. First dorsal pore in furrow 10/11, 11/12. Clitellum *xiii* ($\frac{1}{2}$ *xiii*)–($\frac{1}{2}$ *xvi*) *xvi*, saddle-shaped. Male pores combined with the paired prostatic pores *xvii*, inconspicuous in setal line *b* opening anteriorly in slight concavities on massive muscular paired pads (in the clitellate syntypes these pads form the lateral walls of an invaginated, single, median copulatory pouch); the muscular pads are papillose especially posteriorly when the papillae are more numerous. Female pores paired *xiv* within *aa* about $\frac{1}{3}$ *aa* apart, approximately equidistant from the other and the adjacent seta *a*; located slightly anteriorly to the setal ring. Spermathecal pores paired 8/9, inconspicuous by setal line *b* as slight depressions in paired, massive papillose pads than extend across most of the mid-ventral surfaces of *viii* and *ix*, often obliterating furrow 8/9. In addition to the papillae on the pads associated with the male and spermathecal pores, one syntype has midventral pads in furrows 13/14, 14/15 and 15/16 that carry between four and eight papillae. The mid-ventral surface of *circa xxiv–xxx* is somewhat raised and more heavily pigmented between *bb*.

Setae moderate to stout, widely paired, ventral; post-clitellar formula $aa:ab:bc:cd = 2{\cdot}0:1{\cdot}2:1{\cdot}5:1{\cdot}0$, where $dd =$ three-quarters of the body circumference.

Internal characters. Septa 4/5 and 5/6 strongly thickened, other anterior septa membranous. Gizzards large, strongly muscularized. Intestinal caeca of variable number 6–12 *xxix–xxxiv* to *xxix–xl*. Prostates, single pair *xvii*, highly convoluted filling most of *xviii* and *xix* with a long, muscular ectal region. Single pair of spermathecae in *ix*, with a stout duct and distinct ampulla; two diverticula present on the duct, the lateral diverticulum arises more ectally than the more highly convoluted medial diverticulum. Nephridia: meronephridia throughout the body and a single pair of holonephridia present in each intestinal segment.

TYPE LOCALITY. North Ejura, Ghana.

MATERIAL EXAMINED. 2C* 24A* Near the river, north of Ejura (7°23′n 1°15″W), central Ghana; coll. J.D. Plisko, date? BM(NH) 1984.4.1: 1–26 (syntypes of *Millsonia artesetosa).*

DISTRIBUTION. Known only from the type locality.

REMARKS. The near equidistant location of the setae on the ventral surface and the reduction in the number of strongly muscularized anterior septa may indicate that this is a weakly burrowing species; possibly it is a denizen of forest litter and crevices among tree roots.

Millsonia ashantiensis sp. nov.

(Figs 3C & 4C)

DIAGNOSIS. Spermathecal pores paired in furrow 8/9 in setal line *b* located within a shallow, single median pouch-like vestibule; combined male and prostatic pores paired on segment *xvii*, usually on prominent porophores; female pores paired in the setal ring about $\frac{1}{3}$ *aa* apart within setal lines *aa*; single mid-ventral papillose pads often in furrows (12/13), 13/14, 14/15, 15/16; 16 pairs of intestinal caeca beginning in *xxviii*; paired male copulatory pouches absent; meronephric only.

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*C = clitellate (specimen), A = aclitellate (specimen).

DESCRIPTION. *External changes.* Length (aclitellate specimens 60–255 mm) clitellate specimens 211–330 mm; diameter (aclitellate specimens 2–5 mm) clitellate specimens 5–8 mm. Segments 400–517 (402 in juvenile 60 mm long); commonly triannulate. First dorsal pore 4/5 but very small, large dorsal pores beginning in furrow (11/12) 12/13, 13/14, (14/15). Clitellum $\frac{1}{2}$ *xiii—xvii*, saddle-shaped. Male pores paired combined with the prostatic pores within paired pouches; when the pouches are everted the pores are seen to be carried on large, crenulated porophores occupying most of the ventral surface of *xvii* and encroaching onto *xvi* and *xviii*. Female pores paired in the setal ring of *xiv* within *aa* about $\frac{1}{3}$ *aa* apart; in more mature specimens the body wall deepens locally to produce paired, medially curved longitudinal grooves or a single, short, transverse furrow linking the pores. Spermathecal pores paired 8/9 in setal lines *b*, in mature individuals they are located within a single, shallow, mid-ventral pouch-like vertibule. Oval papillose pads, single mid-ventral sometimes in each of furrows (12/13), 13/14, 14/15, 15/16; usually carrying two papillae. The body-wall on a few segments behind the clitellum usually glandular and raised at least between *bb* on *xviii* and *xix*.

Setae closely paired, ventral; post-clitellar formula $aa:ab:bc:cd = 5:1:4:1$ where $dd =$ two-thirds of the body circumference.

Internal characters. Septa 4/5—11/12 strongly muscularized, 12/13 less so. Gizzards large, of equal size. Intestinal caeca 16 pairs, *xxviii–xliii*. Prostates paired, highly convoluted in *xvii–xix* with a slender muscular ectal portion. Single pair of spermathecae in *ix*, adiverticulate but mostly with nodular areas on the duct; the proximal portion of the duct is dilated and opens medially into a small chamber that communicates with the exterior, the distal portion of the duct gradually enlarges into a clavate ampullla. Nephridia: meronephridia only present.

TYPE LOCALITY. Ayeduasi, near Kumasi, Ghana.

MATERIAL EXAMINED. 7C Ayeduasi village, Kumasi (6°50′N, 1°35′W), Central Ghana; coll. I.K.B. Acheampong, ? date; BM(NH) 1968.2.32–39 (syntypes of *Millsonia ashantiensis*).
2C 3A 7juv. Bomsa village, Kumasi (6°50′N. 1°35′W), central Ghana; coll. J.J. Niles, ? date; (BM(NH) 1968.2.40–51.
1C Afrantwa, Ashanti (7°24′N. 1°57′W.), central Ghana; coll. J.J. Niles, ? date; BM(NH) 1968.2.52.

DISTRIBUTION. Central Ghana.

Millsonia brevicingulata sp. nov

(Figs 9E & 10E)

DIAGNOSIS. Spermathecal pores paired in furrows 7/8/9 in setal line *b*; male pores paired *xviii*, prostatic pores paired *xvii* and *xix* discharging on porophores, the posterior pair being reduced; female pores within *ab* slightly anterior to the setal ring; single mid-ventral papilla on *ix* by furrow 9/10, paired papilla on $\frac{2}{3}$*xii* by setal line *b*, on *xx* within *bc* and on *xxi*, *xxii* and *xxiii* within *aa*, single transverse mid-ventral pad present *xvi* and most of segments *xxiv–xxxv*; 1 pair (occasionally 2 pairs) of intestinal caeca *xxv* (*xxvi*);holo- and meronephric.

DESCRIPTION. *External characters.* Length 46–101 mm, diameter 2–3 mm. Segments 162–218; tetrannulate in the pre-clitellar region, triannulate in the post-clitellar region. First dorsal pore 7/8. Clitellum short, $\frac{2}{3}$*xiii–xviii*, saddle-shaped extending ventrally to below setal line *b*. Male pores paired *xviii* (not seen) discharging into paired seminal grooves passing between paired porophores on *xvii* and *xix* that carry the prostatic pores, each pair is joined by a raised transverse pad, the hinder porophores and pad in *xix* are reduced in size. Female pores paired slightly anteriorly to the setal ring in *xiv* lying between setal lines *ab* close to setal line *b*. Spermathecal pores paired, in furrows 7/8/9 in setal line *b* with a slight swelling of the ventral body wall immediately anterior to the pores. Single mid-ventral papilla usually present on *ix* close to furrow 9/10; paired papillae occur on $\frac{2}{3}$*xii* in setal line *b*, a raised transversely oval pad lies between the ventral margins of the clitellum on segmemt *xvi*, while further papillae are located on *xx* where they are widely paired between setal lines *bc* and closely paired on *xxi*, *xxii* and *xxiii* near to setal line *a*. Thereafter, a series of low transversely oval pads are usually present within *aa* in the setal rings of some or all of the segments back to *xxxv*.

Setae closely paired, ventral; post-clitellar formula *aa* : *ab* : *bc* : *cd* = 7 : 1 : 5 : 1 where *dd* = two-thirds of the body circumference.

Internal characters. First septum 4/5, septa 5/6–10/11 strongly thickened, 11/12 and 12/13 less so. Gizzards strongly muscularized, of equal size; in one syntype the anterior pair of calciferous glands is greatly reduced in size. One or sometimes two pairs of intestinal caeca present *xxv* (*xxvi*). Prostates paired *xvii* and *xix*, slender and highly convoluted with the hinder pair commonly reduced. Spermathecae paired *viii* and *ix*; ampulla globular to conical in shape merging into a stout duct that, at one-third of its length from the ventral parietes, carries a multilocular diverticulum of comparable length. Nephridia: one pair of holonephridia present in each of the clitellar and post-clitellar segments in addition to numerous discrete meronephridia that occur throughout the body.

TYPE LOCALITY. Kumasi, central Ghana.

MATERIAL EXAMINED. 4C 1A Grounds of the State School for Boys, Kumasi (6°50′N, 1°35′W.), central Ghana; Coll. J.J. Niles, 6 May 1966; BM(NH) 1968.2.1–5. (syntypes of *Millsonia brevicingulata*).
3C Forest, Pusu-Pusu, near Abuakwa, Asiakwa Reserve, East Akim (5°50′N. 1°10′W.), central Ghana; Coll. J.D. Plisko,? date; BM(NH) 1984.12.8–10.
1C Alluvium often flooded by the R. Volta, near Brong-Ahafo, north of Bui (8°10′N. 2°20′W.), northwestern Ghana; coll. J.D. Plisko, ? date; BM(NH)1984.12.16.
1C Botanical Gardens, Aburi (5°50′N. 0°11′W.), southern Ghana; coll. J.D. Plisko, ? date; BM(NH) 1984.12.17.
1C Savanna, Wango-Fitini, northern Ivory Coast; coll. P. Lavelle, ? date; BM(NH) 1971.22.113.

DISTRIBUTION. ? Northern Ivory Coast and Ghana.

REMARKS. The specimen from the northern Ivory Coast can be only provisionally assigned to this species due to its immaturity despite the presence of a clitellum; moreover, the diagnostic intestinal caeca, the gonads and seminal vesicles are also absent.

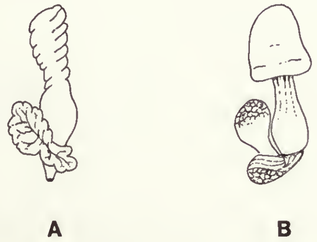

Fig. 2 Spermathecae (not to scale) of *Millsonia* spp. with spermathecal pores in furrow 7/8. (A)*oracapensis*; (B)*hemina*.

Millsonia caecifera (Benham, 1894)

(Figs 7H & 8H)

Benhamia coecifera (lapsus) Benham, 1894: 103; Reynolds & Cook, 1976: 88.
Benhamia caecifera Benham, 1894: 107; Beddard, 1900: 167.
Dichogaster caecifera: Michaelsen, 1900: 366.
Millsonia caecifera: Omodeo, 1958: 600; Sims, 1965*a:* 299.

DIAGNOSIS. Very large worm; spermathecal pores paired in furrows 7/8/9 in setal line *a*; male pores paired *xviii*, prostatic pores inconspicuous, paired *xvii* and *xix*; female pores paired *a* slightly anterior to the setal ring; numerous small papillae clustered over setal lines *ab* on *vii–xiii* and forming a pattern over *xvi–xxiii* within the ventral borders of the elongate clitellum; 24 pairs of intestinal caeca *xxix–lii*; meronephric only.

DESCRIPTION. *External characters*. Length 230 (aclitellate) — 510 mm (holotype), 800 mm (Beddard, 1900), diameter 11–12 mm but wider at the clitellum, up to 17 mm. Segments 310–359, predominantly biannulate with the anterior annulus large, bearing the setae. First dorsal pore 4/5. Clitellum long, *xiii–xxiii*, mostly saddle-shaped extending to setal line *d* by segment *xvi* or *xvii* to below *b* more posteriorly but more or less annular on segments *xiv* and *xv*. Male pores paired *xviii* (not seen) discharging into paired seminal grooves lying within setal lines *bc* that sub-terminally lead medially to the paired, inconspicuous prostatic pores located by setal line *a* on segments *xvii* and *xix*. Female pores paired close to setal line *a* slightly anterior to the setal ring. Spermathecal pores simple, paired in setal line *a* in furrows 7/8/9. Numerous small papillae present on segments *vii–xiii* occurring in paired clusters of two to six papillae mainly across setal lines *ab*; also numerous within the genital field and the ventral borders of the posterior clitellum where they form a distinctive pattern.

Setae closely paired, ventral; post-clitellar formula $aa : ab : bc : cd = 6 : 1 : 5 : 1$ where $dd =$ three-quarters of the body circumference.

Internal characters. First septum 4/5, 4/5–8/9 delicate, 9/10–13/14 greatly thickened, 14/15 and 15/16 less so. Gizzards strongly muscularized, of equal size. Intestinal caeca 24 pairs present *xxix–lii*, the last six or so gradually diminishing in size. Prostates paired in *xvii* and *xix*; slender and moderately convoluted, ectally each with a pronounced delicate muscular duct. Spermathecae paired *viii* and *ix*; ampulla of each is simple and about the same length as the duct, the latter dilating near where it enters the parietes; the posterior spermathecae are slightly larger with a small digitate 'diverticulum' present on the duct. Meronephridia only present being diffuse on the anterior septa and discrete on the parietes of the clitellar and post-clitellar segments.

TYPE LOCALITY. Axim, coast of Ghana.

MATERIAL EXAMINED. *Previously recorded*. 1C Axim (4°51′N. 2°15′W.), coast of southwestern Ghana; coll. Captain Torry, ? date; BM(NH) 1894. 12.31.1 (holotype of *Benhamia caecifera*).
1C (fragments) 'Ashanti' (?vicinity of Kumasi, 6°50′N. 1°35′W.), central southern Ghana; coll. ? date?; BM(NH) 1904.10.5.657 (Beddard, 1900).
New records. 2A Near Kwadaso (6°42′N. 1°39′W), central Ghana; coll. J.D. Plisko, ? date; BM(NH) 1984.12.18–19.

DISTRIBUTION. (?) Southern and central Ghana.

REMARKS. The precise location of the type locality may be open to speculation, since subsequent records of the species are from central Ghana. It is possible that the only connection between the holotype and the currently recognized type locality, Axim, is that the town was either the place of residence of the collector or the port of dispatch to Europe.

The spelling of the name *caecifera* needs comment since Reynolds and Cook (1976) erroneously reverted to the original orthography which was merely a printer's error of transcription. In the original description, the spelling in the title and second paragraph, page 103, (also the 'running head' at the top of each alternate page) was inadvertently printed as '*cœcifera*' whereas the etymologically correct '*cæcifera*' appears on page 107. Clearly the former is in error so the first spelling of the name is not to be retained but that on page 107 should be employed instead (*International Code of Zoological Nomenclature* (3rd edition 1985), Article 32 (b) (i)). In any case there is a first reviser since Beddard (1900)* validated the name *caecifera* Article 24 (C). The author, Benham, a nineteenth-century graduate of Oxford University was, of necessity, well schooled in the classical languages and clearly would not have employed the stem '*coeci-*' in a Latin-derived scientific name to designate a 'caeca-bearing' species. It seems likely that the error arose where the author made use of ligature to join the vowels when writing his original description, subsequently the printer mis-read the '*a*' for an '*o*' in the hand-written manuscript, so '*œ*' was set instead of '*æ*'.

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*Although Michaelsen (1900: 366) indicated that he was correcting the spelling, Beddard's action took priority since his paper was published in the February of 1900 whereas Michaelsen's monograph was not published until the October.

Due to their great size, individuals of this species must be particularly vulnerable to injury and liable to extinction in cultivation. The collection of specimens may prove increasingly difficult if not impossible in time, as more land is developed or ploughed for agriculture.

Millsonia centralis sp. nov.

(Figs 7E & 8D)

DIAGNOSIS. Spermathecal pores paired $\frac{2}{3}$ *vii* and $\frac{2}{3}$ *viii* in setal line *a*; male pores paired *xviii*, prostatic pores paired *xvii* and *xix*; female pores in or slightly above *a* anteriorly to the setal ring on *xiv*; paired papillae posteriorly to each spermathecal pore also one or two pairs between setal lines *bc* on segments *x*, *xi*, *xii*; genital field comprising two concavities, the anterior over segments *xv* and $\frac{1}{2}$ *xvi*, the posterior over segments *xvii*, *xviii*, *xix*, peripheral papillae common; 14 pairs of intestinal caeca *xxix–xlii*; only two pairs of calciferous glands in segments *xvi* and *xvii* (i.e. undeveloped in segment *xv*); meronephric only.

DESCRIPTION. *External characters.* Length 145–200 mm, diameter 4–6 mm. Segments 286–324, commonly regenerating after 75–80; strongly biannular. First dorsal pore 5/6. Clitellum *xii–xix*; saddle-shaped. Male pores paired in *xviii* discharge into paired seminal grooves passing between the (paired) prostatic pores of each side in *xvii* and *xix*; the latter being seen as low papillose porophores in the second of the two concavities that form the genital field, the first, i.e. the anterior concavity, has peripheral papillae and extends between furrow 14/15 and $\frac{1}{2}$ *xvi*. Female pores paired somewhat anteriorly to the setal ring in *xiv*, lying in or slightly above setal lines *a*. Spermathecal pores paired in the hinder regions of segments *vii* and *viii* by setal line *a*; two small papillae occur by the posterior border of each pore while a swollen, transversely oval area may surround each pair of pores. In addition to segmentally paired papillae located peripherally to the genital field, single or double pairs of papillae occur near the posterior furrows of segments *x*, *xi* and *xii* between setal lines *bc*; a single, mid-ventral papilla is sometimes present near the posterior furrow of segment *xix*.

Setae closely paired, ventral; post-clitellar formula $aa:ab:bc:cd: = 4:1:4:1$ where $dd =$ two-thirds of the body circumference.

Internal characters. First septum 4/5, all the anterior septa are membranous until 10/11 and 11/12 which are strongly muscularized with 12/13 and 13/14 less so. Gizzards equal in size and moderately muscularized; only two pairs of calciferous glands seen, occurring in segments *xvi* and *xvii*, i.e. not seen in *xv*. Intestinal caeca present, 14 pairs *xxix–xlii*. Prostates, two pairs, *xvii* and *xix*, each highly convoluted with a slender, muscular portion ectally. Spermathecae paired in *viii* and *ix*, each has a short, stout duct swelling slightly ectally and an elongate, conical ampulla; adiverticulate. Meronephridia only present, being diffuse anteriorly and discrete in the intestinal region.

TYPE LOCALITY. Ayedusa, central Ghana.

MATERIAL EXAMINED. 15C 1A Ayedusa Village (6°40′n. 1°34′W.), central Ghana; coll. I.K.B. Acheampong, 24 Jun, 1967; BM(NH) 1968.2.90–105 (syntypes of *Millsonia centralis*).
1C Bekwaia, central Ghana; coll. J.J. Niles, ? date; BM(NH) 1968.2.106.
2C 1A 'Prempeh College', University of Science and Technology, Kumasi (6°50′N. 1°35′W.), central Ghana; coll. Mary Tazelaar, 21 Mar. 1956; BM(NH) 1984.5.130–132.
1C Under trees of a banana plantation, Kwadaso (6°42′N. 1°39′W.), central Ghana; coll. J.D. Plisko, 31 Mar. 1966: BM(NH) 1984.4.79.
1C Under citrous trees, Kwadaso (6°42′N. 1°10′W.), central Ghana; coll. J.D. Plisko, 7 Jun. 1966; BM(NH) 1984.4.78.
17C 8A Cocoa plantation, Bunso (6°12′N. 1°49′W.), south central Ghana; coll. J.D. Plisko, ? date; BM(NH) 1984.4.53–77.

DISTRIBUTION. Central Ghana.

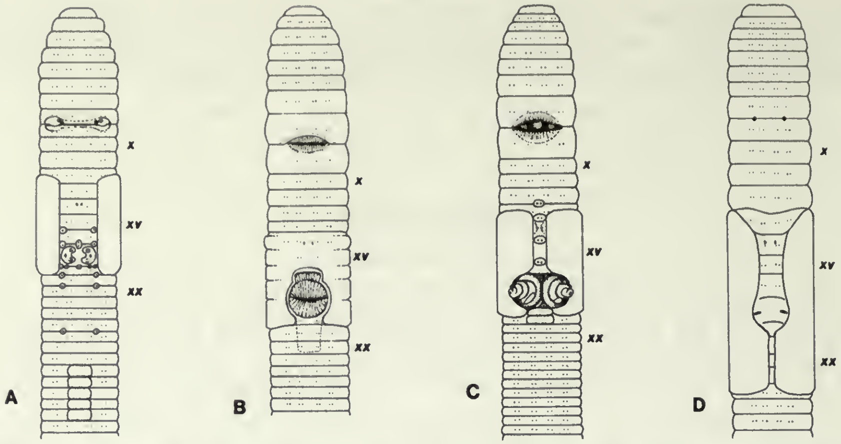

Fig. 3 *Millsonia* spp. with spermathecal pores in furrow 8/9, meronephridia only present (holonephridia absent); anterior region, ventral view (not to scale). (A)*sokodeana*, (B)*nigra*, (C)*ashantiensis* (male field everted); (D)*mima*.

REMARKS. Despite the incomplete expression of the generic characters, i.e. the absence of the anteriormost pair of calciferous glands from segment *xv* (a trend seen in *M. brevicingulata*), I propose to include this species within the genus *Millsonia* since it possesses separate gizzards in *v* and *vi*, and intestinal caeca.

Millsonia cruciventris sp. nov.

(Figs 5E & 6E)

DIAGNOSIS. Spermathecal pores paired in furrow 8/9 in setal lines *ab*; combined male and prostatic pores paired on segment *xvii* (genital field may be invaginated); female pores paired within *aa*, located slightly anteriorly to the setal ring about distance 1·5 *ab* below *a*; male gential field may be invaginated in mature individuals otherwise seen as four (two pairs) of papillose pads; nine pairs of intestinal caeca *xxviii–xxxvi*; holo- and meronephric.

DESCRIPTION. *External characters.* Length 70(? regenerating)—151 mm, diameter 5–7 mm. Segments 189(? regenerating)—295; multiannualte, mostly tetrannulate but further subdivisions common anteriorly; caudal region (?) flattened. First dorsal pore 10/11. Clitellum *xiii–xvii*, saddle-shaped. Male and prostatic pores combined, paired *xvii*; in subadults they lie in setal line *ab* on a narrow, transverse, raised glandular strip that divides the genital field; another but longitudinal glandular strip bisects the transverse strip to form a cross (i.e. a plus sign, +) so causing the field to be composed of four papillose pads. These characters are not seen in mature adults as the genital field invaginates with the papillose pads forming the walls of a large pit-like, single mid-ventral male 'pore' over segments *xvi* and *xvii*. Female pores paired on *xiv* slightly anterior to the setal ring, located within setal lines *aa* about 2 *ab* apart (each about 1·5 *ab* below seta *a*); in mature adults when anterior setae are missing, the female pores are carried on a glandular rectangular pad. Spermathecal pores paired in furrow 8/9 across setal lines *ab*, the hinder annulus of *viii* and the anterior annulus of *ix* are swollen with several (usually one to four) papillae laterally to the spermathecal pores, i.e. in *bc*. Raised transverse pads often present below setal line *b* on up to eight post-clitellar segments, e.g. (*xxiii*) *xxiv–xxvii* (*xxx*).

Setae closely paired, ventral; seldom present in the pre-clitellar and clitellar regions; post-clitellar formula *aa* : *ab* : *bc* : *cd* = 7 : 1 : 3 : 1 where *dd* = three-quarters of the body circumference.

Internal characters. Septa 4/5–10/11 thickened. Gizzards strongly muscularized but disparate in size with the posterior gizzard twice the size of the anterior. Intestinal caeca nine pairs, *xxviii–xxxvi*. Prostates single pair, very long and convulated passing through several segments.

Single pair of seprmathecae in *ix*, with a long, stout duct and pronounced ampulla, lateral diverticulum on the duct poorly developed and may be overlooked. Nephridia: meronephridia present throughout the body with, in addition, paired holonephridia in the intestinal region.

TYPE LOCALITY. Ada Kanyanga, southeastern Ghana.

MATERIAL EXAMINED. 23C 2A Under tomato plants, Ada Kanyanga (5°55′N. 1°10′W.), S.E. Ghana; coll. J.D. Plisko, date ?; BM(NH) 1984.4.80–104. (syntypes of *Millsonia cruciventris*).
6C Cultivated field, Ada Koloidaw (5°40′N. 0°25′W.), S.E. Ghana; coll. J.D. Plisko, date?; BM(NH) 1984.4.105–110.

DISTRIBUTION. Southeastern Ghana.

Millsonia ditheca Sims, 1965

(Figs 9F & 10F)

Millsonia ditheca Sims, 1965*a*: 296.

DIAGNOSIS. Spermathecal pores single, mid-ventral in furrows 7/8/9; male pores paired *xviii*, prostatic pores, inconspicuous, closely paired *xvii* and *xix*; female pore single, mid-ventral $\frac{1}{3}$ *xiv*; paired papillae mainly in setal line *b* in furrows 15/16/17 and *c* in furrow 19/20, occasionally in *a* on segment *viii* and within the genital field; eight pairs of intestinal caeca, *xxvii–xxxiv*; holo- and meronephric.

DESCRIPTION. *External characters*. Length 128–154 mm, diameter 4·5–5 mm. Segments 264–342; tetrannulate in the pre-clitellar region, triannulate in the post-clitellar region. First dorsal pore (10/12) 11/12. Clitellum *xiii–xvii*, saddle-shaped extending ventrally nearly to setal line *d*. Male pores (not seen, *xviii*) discharge into paired grooves passing between inconspicuous, closely paired prostatic pores opening in setal line *a* on segments *xvii* and *xix*. Female pore single, mid-ventral $\frac{1}{3}$ *xiv*.Spermathecal pores single, mid-ventral in furrows 7/8/9, simple. Papillae closely paired in furrows 15/16/17 in setal line *b* and widely paired in furrow 19/20 in setal line c; adventitious papillae common ventrally on the spermathecal segments when sometimes paired in setal line *a*, similarly additional paired papillae often present on segments *xvii* and *xix* medially to the seminal grooves. Raised transverse ridges variably present on segments *xxi–xxii*, largest anteriorly, seldom extending beyond setal line *d*.

Setae closely paired, ventral; post-clitellar formula $aa:ab:bc:cd = 7:1:4:1$ where $dd =$ three-quarters of the body circumference (in the pre-clitellar region the setae are more ventrally situated due to a reduction in setal distances *aa* and *bc*.).

Internal characters. Septa 4/5—10/11 thickened, 11/12 and 12/13 less so. Gizzards strongly muscularized and of equal size. Intestinal caeca, eight pairs present *xxvii–xxxiv*. Prostates paired *xvii* and *xix*, loosely coiled. Spermathecae single in *viii* and *ix*, adiverticulate with the ampulla and duct of about equal length. Nephridia, meronephridia present throughout the body in addition to a single pair of holonephridia in each intestinal segment.

TYPE LOCALITY. Tafo, southeastern Ghana.

MATERIAL EXAMINED. *Previously recorded*. 2C 19A Under cocoa trees, Tafo (6°15′N. 0°20′W.), southeastern Ghana; coll. M. Tazelaar, 26 Oct. 1955; BM(NH) 1964.2.170–188 & 227–232 (holotype and paratypes of *Millsonia ditheca*).
New records. 3C Under grass cuttings, Tafo (6°15′N. 0°20′W.), southeastern Ghana; coll. M. Tazelaar, 1956; BM(NH) 1964.2.233–235.

DISTRIBUTION. Tafo, southeastern Ghana.

Millsonia ghanensis Sims, 1965

(Figs 9C & 10C)

Millsonia ghanensis Sims, 1965*a*: 293.

DIAGNOSIS. Spermathecal pores paired $\frac{3}{4}$ *vii* and $\frac{3}{4}$ *viii* across setal lines *ab*; male pores paired *xviii*,

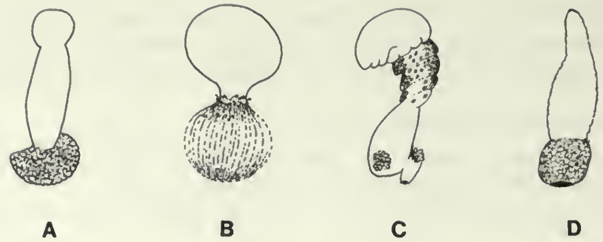

Fig. 4 Spermathecae (not to scale) of *Millsonia* spp. with spermathecal pores in furrow 8/9, meronephridia only present (holonephridia absent). (A)*sokodeana*; (B)*nigra*; (C)*ashantiensis*; (D)*mima*.

prostatic pores paired *xvii* and *xix*; female pores within *aa* nearly $\frac{1}{2}$ *aa* apart anteriorly to the setal ring; papillose pads single, mid-ventral in furrows 9/10–16/17, papillae commonly paired often single or multiple; seven or eight pairs of intestinal setae *xxvii–xxxiii* (*xxiv*); holo- and meronephric.

Description. *External characters.* Length 210–387 mm, diameter 5–9 mm. Segments 262–393, anteriorly commonly biannulate with further subdivision, post-clitellar region strongly triannulate. First dorsal pore 10/11. Clitellum *xiii–xix*, saddle-shaped. Male pores paired *xviii* discharging into paired seminal grooves passing between the (paired) prostatic pores of each side in *xvii* and *xix* (location of the pores difficult to determine). Female pores paired slightly anteriorly to the setal ring of segment *xiv* located within *aa* nearly $\frac{1}{2}$ *aa* apart. Spermathecal pores near the posterior furrows of segments *vii* and *viii*, seen as transverse slits with crenulated lips across setal lines *ab*. Single, mid-ventral papillose pads occur in the furrows between the spermathecal pores and the prostatic pores, i.e. 9/10–16/17; most carry a single pair of papillae, but in the holotype the papilla is single in the first and last and four papillae are present on the pad in furrow 15/16. Mid-ventral pads may be present on the segments immediately behind the clitellum, mostly restricted to below setal line *a* but the more anterior pads may be broader and extend perhaps to setal line *c*; sometimes carrying paired papillae (specimens from the Ivory Coast).

Setae closely paired, ventral; post-clitellar setal formula $aa:ab:bc:cd = 5:1:4:1$, where $dd =$ two-thirds of the body circumference.

Internal characters. Septa 5/6–12/13 strongly thickened, 13/14 less so. Gizzards strongly muscularized and of equal size. Intestinal caeca, seven and sometimes eight pairs present *xxvii–xxxiii* (*xxxiv*). Prostates paired *xvii* and *xix*, highly convoluted and impinging on adjacent segments, each with a slender muscular ectal region. Spermathecae paired *viii* and *ix*, simple, clavate; adiverticulate but the duct with flattened rugose 'wings'. Nephridia: a single pair of holonephridia are present in each intestinal segment in addition to meronephridia present throughout the body.

Type locality. Bunso, central Ghana.

Material examined. *Previously recorded.* 8A Tafo (6°15′N. 0°20′W.), Ghana; coll. M. Tazelaar; BM(NH) 1964.2.161–168.

2C 11A Mud at the side of the R. Wiwi (tributary of the R. Oda that flows into the R. Osin), near Kumasi (6°50′N. 1°35′W.), Ghana; coll. M. Tazelaar, 2 Mar. 1956 and 21 Mar. 1956; BM(NH) 1964.2.145–160 & 216–222.

29C 3A Riveside mud, Bunso (6°12′N. 1°49′W.), Ghana; coll. M. Tazelaar, 14 May 1954; BM(NH) 1964.2.26–46 (holotype and paratypes of *Millsonia ghanensis*) & 1964.2.206–215.

87A Riverside mud, Bunso (6°12′N. 1°49′W.), Ghana; coll. M. Tazellar, 22 Feb. 1951 & 21 Feb. 1952; BM(NH) 1964.2.47–103 & 114–144.

4C 2A Between Kili and Bunso (6°12N. 1°49′W.), Ghana; coll. M. Tazelaar, 21 Feb. 1952; BM(NH) 1964.2.104–113.

1C Apapam (6°10′N. 1°35′W.), Ghana; coll. M. Tazelaar; BM(NH) 1964.2.169.

New records. 2C Savannah with palmira palms (*Borassus*), Lamto, 60 km south of Topumodi (6°32′N. 5°10′W.), southern Ivory Coast; coll. P. Lavelle; BM(NH) 1971.22.70–71.

1A Rich brownish-grey soil, grazing land, Navrongo (10°51′N. 1°03′W.), northern Ghana; coll. J.D. Plisko, ? date; BM(NH) 1984.12.20.
1C Soil in cocoa plantation, Bunso (6°12′N. 1°49′W.), central Ghana; coll. J.D. Plisko, ? date; 1984.12.21.

DISTRIBUTION. Southern Ivory Coast and southern Ghana.

REMARKS. Subadult individuals may prove difficult to identify, see *Remarks* under *M. riparia*.

Millsonia guttata (Michaelsen, 1912)

(Figs 7D & 8C)

Dichogaster inermis guttata Michaelsen, 1912: 28.
Millsonia inermis guttata: Omodeo, 1955: 221.

DIAGNOSIS. Spermathecal pores paired in setal lines *ab* in furrows 7/8/9, but in mature individuals each pair commonly located within a shallow vestibule; male pores paired *xviii* and prostatic pores paired *xvii* and *xix* with the pores of each side discharging into a (paired) longitudinal seminal groove; when the genital field is everted numerous papillae may be seen, also paired spherical processes, on *xvii* and *xix*; female pores paired on *xiv* in setal line *a* slightly anteriorly to the setal ring; ventrally a few scattered papillae may be present; a raised glandular area develops in mature individuals below setal line *a* over several post-clitellar segments; setae closely paired, frequently absent from the anteriormost segments; usually 14 (13–16) pairs of intestinal caeca *xxx*-(*xlii*) *xliii* (*xliv*, *xlv*); meronephric only.

DESCRIPTION. *External characters*. Length 175–280 mm, diameter 5–9 mm. Segments 315–489, mainly triannulate. First dorsal pore 12/13 but may be occluded together with the dorsal pores of the clitellar region. Clitellum ($\frac{1}{2}$ *xii*) *xiii–xix*, saddle-shaped. Male pores paired *xviii* discharging into paired seminal grooves that join the paired prostatic pores in *xvii* and *xix*; the genital field is contained within a copulatory pouch extending from *xvii–xix* but with the aperture confined to *xviii*, however it may become everted during killing, fixing and preserving when its papillose condition and paired spherical processes in *xvii* and *xix* are revealed. Female pores paired in (or adjacent to) setal lines *a* slightly anteriorly to the setal ring; sometimes carried on a slightly raised oval to rectangular area extending laterally to above setal line *b* with a shallow transverse groove joining the pores. Sphermathecal pores paired in furrows 7/8/9 across setal lines *ab*; in mature specimens the furrows may deepen ventrally to form shallow vestibules when the hindermost annuli of *vii* and *viii* usually become raised and seemingly more highly glandular. Papillae, only a few commonly present, usually irregularly scattered but sometimes mid-ventral. Mid-ventral glandular pads may develop below seta *a* on ten or more post-clitellar segments, mainly *xxiv–xxxiii*.

Setae closely paired, ventral; mainly uniform but anteriorly the ventral setae may be somewhat stouter than the lateral setae, while in mature individuals the lateral and the anteriormost ventral setae may be absent from the pre-clitellar region; post-clitellar setal formula $aa : ab : bc : cd = 8 : 1 : 6 : 1$ where $dd =$ two-thirds of the body circumference.

Internal characters. Septa 4/5–11/12 strongly thickened, 12/13 backwards delicate. Gizzards strongly muscularized and of equal size. Intestinal caeca, 13–15 pairs, commonly 14 pairs, present *xxx*–(*xlii*) *xliii* (*xliv*, *xlv*). Prostates paired *xvii* and *xix*, highly convoluted each becoming muscular ectally. Spermathecae paired *viii* and *ix*, simple, digitiform; adiverticulate. Nephridia: only meronephridia present.

TYPE LOCALITY. Atakpame, Togo.

MATERIAL EXAMINED. *Previously recorded*. 2C Atakpame (7°34′N. 1°14′E.), Togo; coll. Stockhausen, Jun. 1910; Hamburg V. 3729 (syntypes of *Dichogaster inermis guttata*).
New records. 7C 2A Volta region, eastern Ghana; coll. K. El-Duweini, Mar. 1967; BM(NH) 1968.2.6–12.

OTHER RECORDS. 5C Man (7°31′N. 7°37′W.), western Ivory Coast; Oct./Nov. 1953/4, (Omodeo, 1955: 221).

DISTRIBUTION. Southern Ivory Coast, Ghana and Togo.

Millsonia hemina Sims, 1965

(Figs 1B & 2B)

Millsonia hemina Sims, 1965*a*: 291.

Diagnosis. Spermathecal pores in furrow 7/8 in setal lines *b*; combined male and prostatic pores paired on segment *xvii*; female pores paired between setal lines *a* and *b* slightly anteriorly to the setal ring; papillae common in the pre-clitellar region and transverse pads between setae *aa* in six to twelve post-clitellar segments; two pairs of intestinal caeca *xxiv* or *xxv*, occasionally (?) more posteriorly to, perhaps, *xxvi* or *xxvii*; holo- and meronephric.

Description. *External characters*. length 36–89 mm, diameter 1·5–3·0 mm. Segments 128–189; mostly triannulate but becoming pentannulate in the pre-clitellar segments by the subdivision of the anterior annulus. First dorsal pore 8/9, 9/10. Clitellum (*xii*) $\frac{1}{2}$ *xiii*–$\frac{1}{2}$ *xvii* (*xvii*), saddle-shaped. Male pores paired *xvii*, united with the prostatic pores to form a short oblique slit from setal line *a*

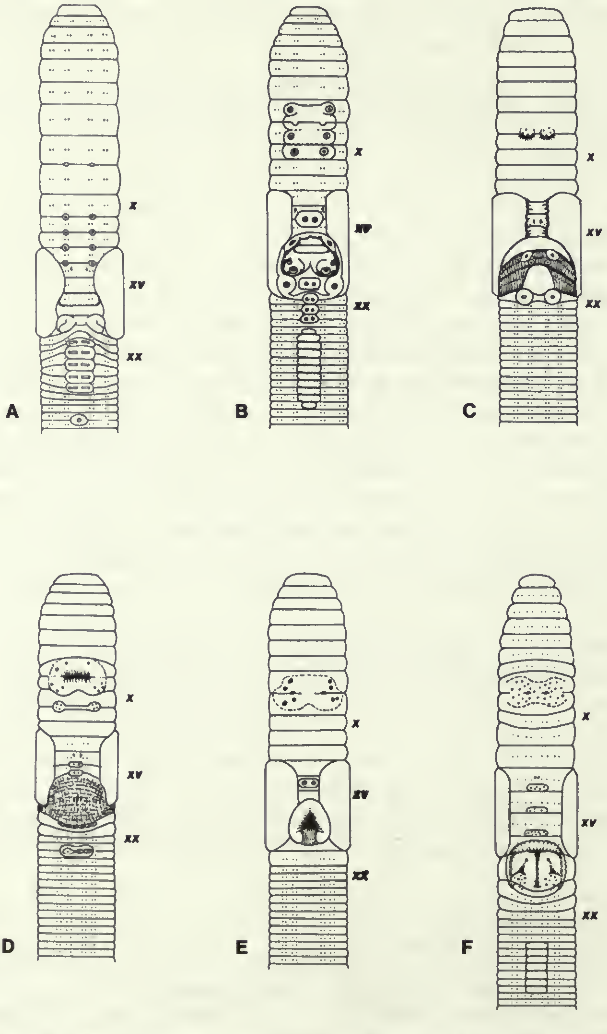

Fig. 5 *Millsonia* spp. with spermathecal pores in furrow 8/9, meronephridia and holonephridia present; anterior region, ventral view (not to scale). (A)*nota*; (B)*hortensis*; (C)*jadwigae*; (D)*moderata*; (E)*cruciventris*; (F)*artesetosa*.

crossing setal line *b* and carried on paired porophores usually encircled by several (four or five) small papillae or carried on a low transverse ridge. Female pores paired *xiv* midway between setal lines *ab* slightly anteriorly to the setal ring. Spermathecal pores paired 7/8 in setal line *b* but stretching more laterally in mature individuals. Papillae common in the pre-clitellar region near setae *ab* and sometimes joined on a low transverse ridge, occasionally papillae single on each segment, even mid-ventral; in the clitellar region paired papillae usually on *xvi* but more closely paired immediately behind the clitellum (*xviii*, *xix* and *xx*) and may be fused mid-ventrally. Ventral surface between setal lines *aa* raised to form transverse genital pads on at least segments *xxii–xxvi*, perhaps to *xx–xxxi*.

Setae closely paired, ventral; post-clitellar formula $aa:ab:bc:cd = 5:1:4:1$ with *dd* approaching two-thirds the body circumference.

Internal characters. Septa 4/5–11/12 strongly thickened. Gizzards of equal size. Intestinal caeca, two pairs present, the first usually in segment *xxiv* with a second pair in *xxv*, occasionally located more posteriorly *xxvi* or *xxvii*, often the hinder pair is imperfectly developed. Prostates paired in *xvii* only, tubular, long and convoluted. One pair of spermathecae in *viii*; duct short with distal and lateral multilocular diverticula; ampulla simple, long and tubular. Nephridia; meronephridia present throughout the body with, in addition, a pair of holonephridia in each segment in the intestinal region.

TYPE LOCALITY. Apapam, southern Ghana.

MATERIAL EXAMINED. *Previously recorded*. 2C 4A Apapam (6°10′N. 1°35′W.), southern Ghana; coll. M.A. Tazelaar, ? date; BM(NH) 1964.2.20–25 (holotype and paratypes of *Millsonia hemina*).

New records. 5C 4A Kuntanasi, near Lake Bosumtwe (6°30′N. 1°25′W.), southern Ghana; coll. J.J. Niles, 8 Apr 1966; BM(NH) 1968.2.17–25.

3C Deep in mineral soil in rain forest with water pools nearby stream, Kade, Ghana; coll. M.J. Proszynscy 12 Jul. 1964; BM(NH) 1984.4.120–121.

2A Rubber plantation, Bunso (6°12′N. 1°49′W.), southern Ghana; coll. J.D. Plisko, date?; BM(NH) 1984.4.118–119.

6C Cocoa plantation, Bunso, southern Ghana; coll. J.D. Plisko; date?; BM(NH) 1984.4.113–117.

2C Primary forest, Pusu-Pusu, Asiakwe Reserve, near East Akim (5°50′N. 1°10′W.), Abuakwe, southern Ghana; coll. J.D. Plisko, date?; BM(NH) 1984.4.111–112.

6C Nyakrom, near Swedru on the road from Winely to Kpandu, Ghana; coll. J.D. Plisko, date?; BM(NH) 1984.4.122–127.

DISTRIBUTION. Southern Ghana.

REMARKS. A variable species particularly in the presence of, and patterns formed by, the papillae both in the pre-clitellar region and in the genital field. Most specimens examined have paired papillae on the pre-clitellar segments together with discrete male porophores but sometimes the pre-clitellar papillae are single, even mid-ventral, and the male porophores are joined by a transverse ridge. These latter variants are present among the series from the Bosumtwe area. The location of the caeca can be difficult to determine depending on the fixation techniques employed by the collector, but it does seem that sometimes the caeca do occur more posteriorly, perhaps as far back as segment *xxvii*.

Millsonia heteronephra (Michaelsen, 1897)

(Figs 9A & 10A)

Benhamia heteronephra Michaelsen, 1897: 22.
Dichogaster heteronephra: Michaelsen, 1900: 365.
Millsonia heteronephra: Omodeo, 1955: 219; Omodeo, 1958: 59; Sims, 1965*a*: 299.

DIAGNOSIS. Spermathecal pores paired in furrows 7/8/9 near the mid-lateral lines (i.e. above setal line *d*) each with a single antero-ventral papilla; male pores paired *xviii*, prostatic pores paired *xvii* and *xix* (in mature, preserved specimens the pores of each side are carried on laterally displaced swollen pads formed by the eversion of pouches on the left and right sides of the genital field); female pores paired at distance *ab* below setal line *a*, slightly anterior to the setal ring; paired papillae in setal line *a* present in furrows 12/13–15/16; six or seven pairs of intestinal caeca *xxvi–xxxi* (*xxxii*); holo- and meronephric.

DESCRIPTION. *External characters*. Length 251–336 mm, diameter 6–9 mm. Segments 518–580 (? 600), multiannulate with a variable number of annuli anteriorly but triannulate behind the clitellum. First dorsal pore (10/11) 11/12. Clitellum (*xiii*) *xiv–xix* (*xx*), saddle-shaped extending ventrally to below setal line *c* but possibly to *a* anteriorly. Male pores paired *xviii*, in mature individuals they are located in genital pits or pouches that in preserved specimens may become everted; the pores can be seen above setal line *d* discharging into short lateral grooves that join paired longitudinal seminal grooves passing between inconspicuous paired prostatic pores in *xvii* and *xix*. Female pores paired *xiv*, located at distance *ab* below setal line *a* and slightly anterior to the setal ring. Spermathecal pores paired laterally above setal line *d* in furrows 7/8/9; in mature individuals tumid lips develop and a simple papilla appears antero-ventrally to each pore. Paired papillae present in setal line *a* in furrows 12/13–15/16. Raised transverse pads sometimes occur ventrally below setal line *b* on segments *xxi*, *xxii* and perhaps more.

Setae closely paired, ventral; post-clitellar formula $aa:ab:bc:cd = 8:1:3:1$ where $dd =$ two-thirds of the body circumference.

Internal characters. Septa 5/6–10/11 very thick, 11/12 less so. Gizzards unequal with the hinder being slightly larger and more strongly muscularized. Intestinal caeca, six, usually seven pairs present *xxvi–*(*xxxi*) *xxxii*. Prostates paired *xvii* and *xix*, large and strongly convoluted, ectally with a long slender muscular region. Spermathecae paired *viii* and *ix* lying on the lateral parietes, ampulla and duct of about equal length; adiverticulate. Nephridia: one pair of holonephridia in each of the post-clitellar segments together with numerous meronephridia that also occur in the pre-clitellar and clitellar segments.

TYPE LOCALITY. Misahohe, Benim.

MATERIAL EXAMINED. *Previously recorded*. 1C (immature) 'Misahohe Station', Misahohe (6°59′N. 0°40′E.), Benim; coll. Ernst Baumann, 10 Nov. 1893; Hamburg V. 4520 (syntype of *Benhamia heteronephra*, other two syntypes originally reported, not found Zoologisches Institut und Zoologisches Museum, Universität Hamburg, September 1982).

New records. 2C (anterior fragments), 2A 1 juv. Maize plantation, Akoto Ambiente east of Bibiani (6°30′N. 2°08′W.), near the road from Kumasi, southern Ghana; coll. J.D. Plisko, 8 Jun. 1966; BM(NH) 1984.12.11–15.

DISTRIBUTION. Southern Benim and southern Ghana.

REMARKS. The outstanding feature of *M. heteronephra* is that the male genital field becomes grossly developed with the onset of sexual maturity when the male and prostatic pores are displaced laterally until the left and right sides of the field can be directly applied to the widely paired, laterally situated spermathecal pores of a partner during copulation. (The surviving syntype is immature and the male genital field is only poorly developed with the male and prostatic pores still located somewhat ventrally.)

There is a discrepancy between the morphologies of the specimens described above and Michaelsen's original description. In the specimens examined from Ghana, the location of the intestinal caeca can be established with certainty between the segments *xxvi–xxxi*, whereas Michaelsen recorded their presence in *xxxvi–xli*, i.e. ten segments more posteriorly. (Although he recorded six pairs of caeca, he stated that seven pairs were present and, in 1900, he commented that there may be one or two pairs more.) Unfortunately, the anterior intestine with the caeca has been removed from the surviving syntype so the discrepancy cannot be resolved.

However, I am of the opinion that on this occasion a *lapsus calami* occurred and that Michaelsen made a clerical error. His description, and the sole syntype, otherwise match closely the specimens from Akoto Ambiente. In any case, the location of the caeca recorded by Michaelsen would be far more posterior than is usual among other species where the caecal series commonly begins in or nearby segment *xxvi*. If new material should be discovered with caeca located as described by Michaelsen, then clearly the identity of the present series and the relationship with the new material will need careful appraisal.

Millsonia hortensis sp. nov.

(Figs 5B & 6B)

DIAGNOSIS. Spermathecal pores paired in furrow 8/9 in setal line *b*; combined male and prostatic pores paired on segment *xvii*; female pores paired between setal lines *a* and *b* anteriorly to the setal ring; papillae widely paired near to setal line *b* on segments *viii–x*, *xvi* and *xviii*, closely paired on a mid-ventral pad in each of furrows 14/15, 18/19 20/21, 21/22 and on segment *xviii*; four or five pairs of intestinal caeca (either or both the first and last pair may be greatly reduced in size) *xxvi–xxx*; holo- and meronephric.

DESCRIPTION. *External characters*. Length 142–252 mm (88 mm regenerating), diameter 4–5 mm. Segments 212–272 (111 regenerating); triannulate, caudal region slightly swollen. First dorsal pore in furrow 9/10 or 10/11. Clitellum *xiii–xvii*, saddle-shaped. Male pores paired combined with the prostatic pores above setal line *b* on *xvii*, each is carried on a porophore and seen as a transverse slit with flap-like lips, the posterior lip in particular being more fully developed. Female pores paired on *xiv* where they are located anteriorly to the setal ring between setal lines *a* and *b*. Spermathecal pores paired in furrow 8/9 in setal line *b*. Papillae paired on segments *viii–x*, *xvi* and *xviii* nearby or slightly above setal line *b*, each on a raised circular glandular area; raised mid-ventral pads each with two, closely paired, papillae in furrows 14/15, 18/19, 20/21, 21/22 and on segment *xviii*. Mid-ventral surface heavily pigmented and glandular between setal lines *aa* over segments (*xxiii*, *xxiv*) *xxv–xxxii* (*xxxiii*).

Setae closely paired, ventral; post-clitellar formula $aa:ab:bc:cd = 6:1:4:1$ where $dd =$ two-thirds of the body circumference.

Internal characters. Septa 4/5–11/12 strongly muscularized. Gizzards highly muscular and of equal size. Four to five pairs of intestinal caeca present in *xxvi–xxx*, the first and/or the last pairs may be reduced in either diameter or length. Prostates, single pair highly convoluted lying mainly in *xviii* ectally with a muscular duct that passes forwards into the ventral parietes of *xvii*. Spermathecae paired in *ix*, duct long and stout with a large distal ampulla, diverticulum multiocular located midway along the duct; the duct may be convoluted or lead across the segment so that the ampulla of the right spermatheca may lie against the lateral parietes of the left side and *vice versa* the ampulla of the left spermatheca lie by the right parietes. Nephridia: meronephridia present throughout the body with a single pair of holonephridia additionally present in each segment throughout the intestinal region.

TYPE LOCALITY. Botanic Garden, Aburi, southern Ghana.

MATERIAL EXAMINED. 4C Botanic Garden, Aburi (5°50′N. 0°11′W.), southern Ghana; coll. J.D. Plisko, date? BM(NH) 1984.4.128–131 (syntypes of *Millsonia hortensis)*.

DISTRIBUTION. Known only from the type locality.

Millsonia inermis (Michaelsen, 1892)

(Figs 7C & 8E)

Benhamia inermis Michaelsen, 1892: 209; Beddard, 1895:568.
Dichogaster inermis: Michaelsen, 1900: 366; Michaelsen, 1937: 501.
Dichogaster inermis typica Michaelsen, 1912: 28.
Millsonia inermis: Omodeo, 1958: 59; Sims, 1965*a*: 299.

DIAGNOSIS. Spermathecal pores paired by the posterior borders of segments *vii* and *viii* ('7/8/9'), in adults each pair opens into a median vestibule whereas in subadults they are superificial and located slightly above setal line *b*; male pores paired *xviii*, prostatic pores paired *xvii* and *xix* within a deeply invaginated male field; female pores paired within *aa* about distance $\frac{1}{2}$ *ab* below *a* and somewhat anterior to the setal ring; paired papillae usually present slightly above setal line *b* by the posterior borders of segments *ix–xxiii*, in subadults additional paired papillae often medially to the spermathecal pores; usually 14 pairs of intestinal caeca present, occasionally less perhaps 11 pairs (*xxviii*, *xxix*) *xx–xl* (*xli*, *xlii*, *xliii*); meronephric only.

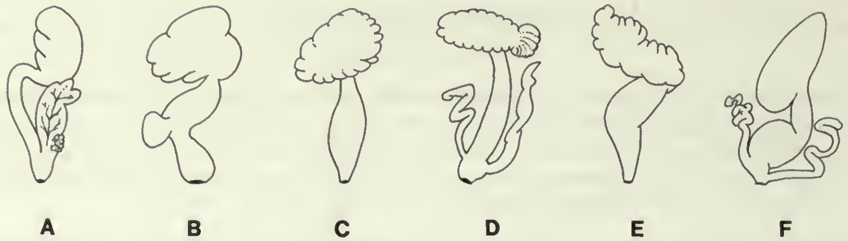

Fig. 6 Spermathecae (not to scale) of *Millsonia* spp. with spermathecal pores in furrow 8/9, meronephridia and holonephridia present. (A)*nota*; (B)*hortensis*; (C)*jadwigae*; (D)*moderata*; (E)*cruiciventris*; (F)*artesetosa*.

DESCRIPTION. *External characters.* Length 123–364, diameter 4–10 mm. Segments 365–384 (regenerating individuals common but 384 segments in one aclitellate, (?) juvenile 123 mm long), mainly triannulate but further subdivision common in the pre-clitellar region. First dorsal pore 12/13 (13/14) occasionally occluded in the clitellar region when the first dorsal pore occurs at the posterior border of the clitellum. Clitellum *xii–xix*, saddle-shaped. Male pores paired *xviii* discharging into paired seminal grooves joining the paired prostatic pores in *xvii* and *xix*; in fully mature specimens the seminal grooves are hidden within a deeply invaginated genital field but in subadults the grooves may be seen lying between setal lines *b* and *c*. The genital field is encircled by a raised rim with a single median anterior papilla and paired posterior papillae, within the invagination two pairs of papillae may often be seen lying medially to the seminal grooves. Female pores paired *xiv* within *aa* about distance $\frac{1}{2}$ *ab* from *a* located slightly anteriorly to the setal ring. Spermathecal pores paired in the hinder regions of segments *vii* and *viii* in the anterior walls of furrows 7/8/9 about distance *ab* above setal line *b*; two pairs of associated papillae commonly present on each of segments *vii* and *viii*, the first pair are located at the same level as the spermathecal pores but lie within *aa* while the second pair are adjacent but located more anteriorly and medially. Paired papillae usually present near the posterior borders of most of segments *ix–xxii* (except in the genital field) lying slightly above the setal line *b*, sometimes the papillae may be multiple.

Setae closely paired, ventral; post-clitellar formula $aa:ab:bc:cd = 5:1:4:1$ where $dd =$ two-thirds of the body circumference. Setae in the clitellar region often with the setal couples on raised genital tumescences.

Internal characters. Septa 4/5–11/12 greatly thickened, 12/13 and 13/14 less so. Gizzards strongly muscularized and of equal size. Intestinal caeca 14 pairs present sometimes fewer (11) located (*xxviii*, *xxix*) *xxx–xl* (*xli–xliii*), the posteriormost three pairs are commonly shorter and arise more laterally. Prostates paired *xvii* and *xix* highly convoluted with a slender muscular portion ectally; the hinder pair are commonly smaller than the anterior pair. Spermathecae paired *viii* and *ix*, basically digitiform but the distal part may be slightly dilated to form an ampulla-like swelling; adiverticulate. Nephridia: only meronephridia present.

TYPE LOCALITY. Adeli, Togo.

MATERIAL EXAMINED. *Previously recorded.* 1C Kete Krachi (7°47′N. 0°50′W.), eastern Ghana; coll. Mischlich, ? date; Hamburg V. 7639 (Michaelsen, 1912: 28).

2C Korle Bu, Accra (5°33′0°15′W.), southern Ghana; coll. S.F. Woodward, Jun 1934; BM(NH) 1935.2.8.1–2 (Michaelsen, 1937: 501).

New Records. 40C 6A Rich brownish-grey soil, pasture, Nvarongo (10°51′N. 1°03′W.), northern Ghana; coll. M.J. Proszynscy, 27, 28 Aug 1963; BM(NH) 1984.4.348–395.

5C 2A Near Bolgatanga (10°44′N. 0°53′W.), beside road to Bawku, northern Ghana; coll. M.J. Proszynscy, 19 Jun 1964 (at the beginning of the rainy season); BM(NH) 1984.4.132–138.

22C 11A Meadow of the Agricultural Station, Koissena Nankani, Nuwronga (10°10′N. 0°05′W.), northeastern Ghana; coll. J.D. Plisko, 24 Aug 1965; BM(NH) 1984.4.283–315.

5C Field of maize, South Mampressi, Wale-Wale (10°20′N. 0°45′W.), beside road from Tamale to Bolgatanga, northern Ghana; coll. J.D. Plisko, 23 Jul 1965; BM(NH) 1984.4.176–180.

20C 2A Field of maize adjoining road, south Mampressi, Wale-Wale (10°20′N. 0°45′W.), between Tamale and Bolgantangi, northern Ghana; coll. J.D. Plisko, 23 Aug 1965; BM(NH) 1984.4.189–210.
1C Agricultural Station, Ejura (7°23′N. 1°15′W.), west central Ghana; coll. J.D. Plisko, 16 Aug 1966; BM(NH) 1984.4.172.
1C 1A By the river, north of Ejura (7°23′N. 1°15′W.), west central Ghana; coll. J.D. Plisko 17 Aug 1966; BM(NH) 1984.4.153–154.
3C 4A Picked up from the road (a.m. and noon) during dry weather, Ejura (7°23′N. 1°15′W.), west central Ghana; coll. J.D. Plisko, 9 Nov 1966; BM(NH) 1984.4.341–347.
4C Field, Ejura (7°23′N. 1°15′W.), west central Ghana; coll. J.D. Plisko, Feb 1967; BM(NH) 1984.4.185–188.
2C Campus, 'Prempeh College' (= University of Science and Technology), Kumasi (6°50′N. 1°35′W.), central Ghana; coll. W. Bellfield, 16 Oct 1957; BM(NH) 1983.41.1–2.
2C 1A By the Abu River, Kumasi (6°50′N. 1°35′W.), central Ghana; coll. J.D. Plisko, date ?; BM(NH) 1984.4.173–175.
1C Garden, Kpeve (6°40′N. 0°20′E.), Volta region, southeastern Ghana; coll. J.D. Plisko, date ?; BM(NH) 1984.4.181–182.
2C 1A Soil under oil palm trees, Kpeve (6°40′N. 0°20′E.), Volta region, southeastern Ghana; coll. J.D. Plisko, date ?: BM(NH) 1984.4.139–141.
4C 2A Roots of a plant beside a stream, Edward Han (6°24′N. 1°32′W.), central Ghana; coll. J.D. Plisko, 25 Aug. 1965; BM(NH) 1984.4.142–147.
1C Kpong (6°11′N. 0°09′E.), southeastern Ghana; coll. J.J. Niles, 18 Jul 1964; BM(NH) 1965.1.1.
6C 16A Pineapple plantation, Manjia, Krombo, Agor Kotea, Kpong (6°11′N. 0°09′E.), southeastern Ghana; coll. J.D. Plisko, date ?: BM(NH) 1984.4.241–262.
8C 13A In soil of flooded paddy fields, Sugar Products Corporation, Kpong, (6°11′N. 0°09′E.), southeastern Ghana; coll J.D. Plisko, date ?; BM(NH) 1984.4.220–240.
11C 9A Rice plantation, Sugar Products Corporation, Kpong (6°11′N. 0°09′E.), southeastern Ghana; coll. J.D. Plisko, date ? BM(NH) 1984. 4.263–282.
20C 5A Ditch beside sugar cane plantation, Kpong (6°11′N. 0°09′E.), southeastern Ghana; coll. J.D. Plisko, 4 Nov 1965; BM(NH) 1984.4.316–340.
2C 2A Soil under sugar cane, Kpong (6°11′N. 0°09′E.), southeastern Ghana; coll. J.D. Plisko, 18 May 1966; BM(NH) 1984.4.168–171.
2C Soil in bush near Somanya (5°55′N. 2°05′W.), southwestern Ghana; coll. J.D. Plisko, 31 Jul 1965; BM(NH) 1984.4.155–156.
2C 7A Sugar cane plantation Yilo Krobo, Osudoku, Somanya (5°55′N. 2°05′W.), southwestern Ghana; coll. J.D. Plisko, date ?: BM(NH) 1984.4.157–165.
5C Copse on the slope of Green Hill, Legon, near the road to Achimoto (5°35′N. 0°15′E.), southern Ghana; coll. J.D. Plisko, date ?; BM(NH) 1984.4.148–152.
2C Soil in the bush between Legon and Achimoto (5°35′N. 0°15′E.), southern Ghana; coll. J.D. Plisko, date ?; BM(NH) 1984.4.183–184.
1C 1A On the surface of the soil after heavy rain, Botanical Garden, Legon (5°33′N. 0°15′E.), southern Ghana; coll. J.D.Plisko, date ?: BM(NH) 1984.4.166–167.
9C Deep in black soil under long grass and trees, south of Legon near Accra (5°33′N. 0°15′W.), southern Ghana; coll. J.M. Proszynscy, 6 Jul 1963; BM(NH) 1984.4.211–219.

Other records. 1C 'Adeli, near Bismarckburg, Togo' (? = near Dutukpene (8°09′N. 0°31′E.), eastern Ghana); coll. Büttner, 20 Sept 1890; Berlin 2153 (holotype of *Benhamia inermis*).
1? 'Mangu District, Togo'; coll. Thierry, 15 Mar 1899 (Michaelsen, 1912: 28).
1? Sokode (8°59′N. 1°11′E.), Togo; coll. F. Schröder, Aug 1900 (Michaelsen, 1912: 28).

Distribution. Ghana and Togo.

Millsonia jadwigae sp. nov

(Figs 5C & 6C)

Diagnosis. Spermathecal pores paired in furrow 8/9 in setal lines *ab*; combined male and prostatic pores paired on segment *xvii* discharging through porophores each with an adjacent postero-medial papilla; female pores paired within *aa*, located slightly anteriorly to the setal ring and distance 2 *ab* below seta *a*; male genital field *not* invaginated with the pores partly enclosed anteriorly by a crescentic pad on segment *xvi* and a trapezoidal pad on *xviii*; seven pairs of intestinal caeca with sometimes a supernumerary pair *xxviii*–*xxxiv* (*xxxv*); holo- and meronephric.

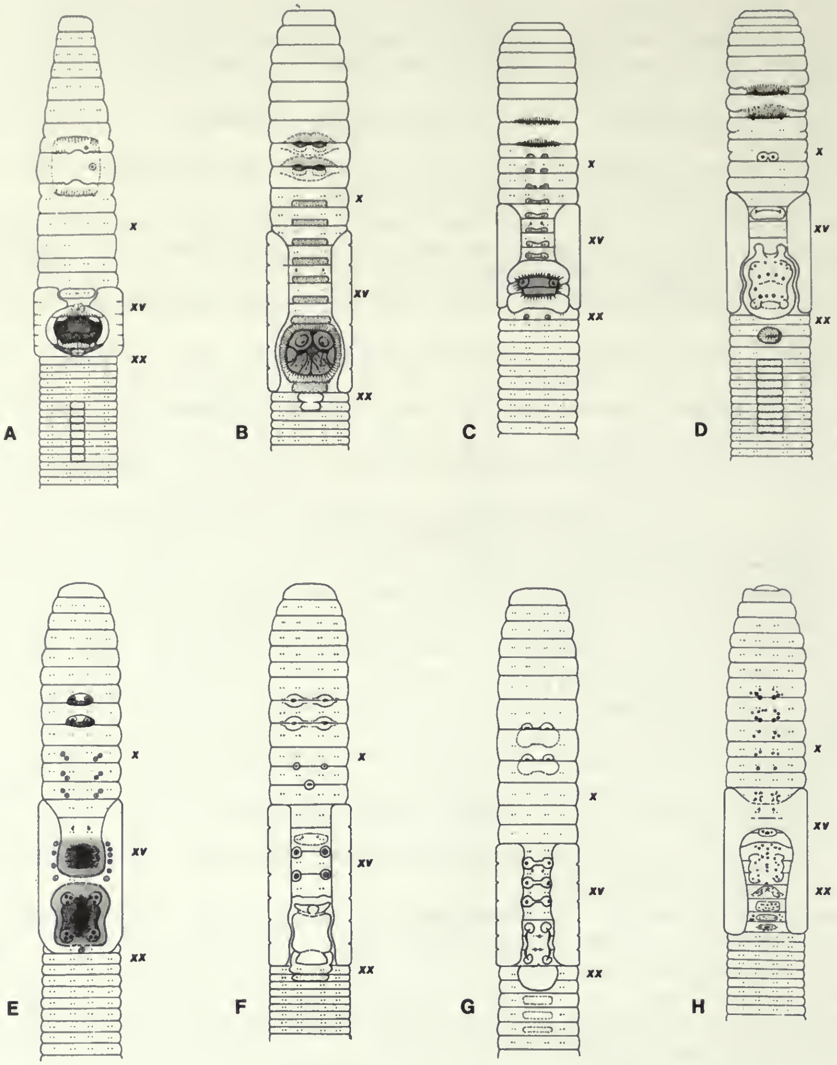

Fig. 7 *Millsonia* spp. with spermathecal pores in furrows 7/8/9 meronephridia only present (holonephridia absent); anterior region, ventral view (not to scale). (A)*nilesi*; (B)*pulvillaris*; (C)*inermis*; (D)*guttata*; (E)*centralis*; (F)*riparia*; (G)*pumilia*; (H) *caecifera*.

DESCRIPTION. *External characters.* Length 69–195 mm, diameter 5–7 mm. Segments 205–265, predominantly triannulate; caudal region commonly flattened or swollen. First dorsal pore in furrow 9/10. Clitellum *xiii*–$\frac{1}{2}$ *viii*, saddle-shaped. Male pores combined with the paired prostatic pores on *xvii*, each on a low porophore above setal line *b* and antero-lateral to a pair of small papillae. Female pores paired *xiv* within *aa* slightly anterior to the setal rin, 3*ab* apart, i.e. distance 2*ab* below setal line *a*. Spermathecal pores paired 8/9 across setal lines *ab*, commonly with paired papillae near the equators of segments *viii* and *ix* also often paired papillae in the anterior wall of furrow 8/9 obscuring the spermathecal pores. Genital field comprises the ventral region of segment *xvi* within the borders of the clitellum being raised into a crescentric pad, the anterior half of segment *xvii* with paired porophores (carrying the male and prostatic pores) and the posterior half with paired papillae slightly closer together than the porophores, the mid-ventral region of segment *xviii* is raised up into a trapezoidal pad while posteriorly segment *xix* is swollen with a pair of papillae about the same distance apart as the porophores on *xviii*. Other post-clitellar genital markings occur as raised transverse pads between setal lines *aa* on segments (*xxiii*) *xxiv–xxx* (*xxxi*).

Setae closely paired, ventral, commonly absent from some or all of the pre-clitellar segments; post-clitellar formula $aa : ab : bc : cd = 5 : 1 : 4 : 1$ where *dd* is three-quartersof the body circumference.

Internal characters. Septa 4/5–10/11 moderately thickened, septa 11/12 and 12/13 less so. Gizzards strongly muscularized but disparate in size with the posterior gizzard considerably larger. Intestinal caeca, 7, possibly 8, pairs present *xxviii–xxxiv* or *xxxv*, although the anterior cacea are clearly digitiform structures, they regress in size posteriorly and the hindermost may be difficult to discern. Prostates, single pair, long and convoluted occupying most of segments *xvii* and *xviii* with a long muscular ectal duct entering the parietes in *xvii*. Single pair of spermathecae in segment *ix*, each with a simple, long duct (diverticulum not seen) and a well-differentiated ampulla having a diameter several times greater than that of the duct. Nephridia: meronephridia present throughout the body; paired holonephridia additionally present in each segment of the intestinal region.

TYPE LOCALITY. Legon, (near the University of Legon), southeastern Ghana.

MATERIAL EXAMINED. 7A 6C Cultivated soil, near the University of Legon, Legon, S.E. Ghana; coll. J.D. Plisko, date ?: BM(NH) 1984.4.396–408 (syntypes of *Millsonia jadwigae*).
2C Expelled by heavy rain from soil under trees in the Botanical Garden Legon, S.E. Ghana; coll. J.D. Plisko, date ?; BM(NH) 1984.4.434–435.
1C 2A Green Hill, Legon, S.E. Ghana; coll. J.D.Plisko, 26 Jun. 1965; BM(NH) 1984.4.452–455.
20C 5A Cultivated soil in a small garden, 5 km ('3 mls') from Legon, S.E. Ghana; coll. J.D. Plisko, 16 Jul. 1965; BM(NH) 1984.4.409–433.
11C 1A Botanical Gardens, Aburi, S.E. Ghana; coll. J.D. Plisko, date?; BM(NH) 1984.4.436–448.
3C Pasture with brownish-grey, rich soil, Nvaronga (10°51'N. 1°03'W.), northern Ghana; coll. J.D. Plisko, date?; BM(NH) 1984.4.449–451.

DISTRIBUTION. Ghana.

REMARKS. This species is named in honour of Dr Jadwiga Danuta Plisko Winkworth, now of Durban, South Africa.

Millsonia lamtoiana Omodeo & Vaillaud, 1967

(Figs 9G & 10G)

Millsonia lamtoiana Omodeo & Vaillaud, 1967: 932.

DIAGNOSIS. Spermathecal pores paired in furrows 7/8/9 over setal lines *ab*; male pores paired *xviii*, prostatic pores paired *xvii* and *xix*; female pores closely paired, midventral; double papillae on single, mid-ventral pads *xiv*, *xv*, *xvi* and (?) *xx*; 19 pairs of intestinal caeca *xxviii–xlvi*; holo- and meronephric.

DESCRIPTION. *External characters.* Length 300 mm (415 mm Ghana), diameter 7–9 mm. Segments 293 (574 Ghana). First dorsal pore 5/6. Clitellum *xiii–xx*, saddle-shaped. Male pores paired *xviii* (not seen) discharging into paired seminal grooves that pass between paired porophores carrying the prostatic pores in setal lines *ab* of segments *xvii* and *xix*. Genital field depressed with three papillae lying obliquely laterally to the posterior porophores; becoming tessellated with maturity. Female pores closely paired by the mid-ventral line of segment *xiv*. Spermathecal pores paired across setal lines *ab* in furrows 7/8/9; as the worms mature so each furrow deepens by each pore to form at first shallow paired vestibules then later a deeper single transverse vestibule. Mid-ventral pads carrying paired papillae usually occur on the hinder surface of the segments by furrows (12/13) 13/14–15/16 and in furrows 21/22–25/26, small papillae sometimes present in furrow 19/20.

Setae very small, closely paired, ventral; post-clitellar formula $aa : ab : bc : cd = 6 : 1 : 5{\cdot}5 : 1$ where $dd =$ two-thirds of the body circumference.

Internal characters. Anterior septa greatly thickened back to 13/14. Gizzards large and highly muscularized. Intestinal caeca, 19 pairs present *xxviii–xlvi*. Prostates paired *xvii* and *xix*. Spermathecae paired *viii* and *ix*, the duct, of similar length to the ampulla, is adiverticulate and globular in shape whereas (in the types) the ampulla bears a digitate diverticulum. Nephridia: meronephridia present throughout the body, additionally each post-clitellar segment contains a pair of holonephridia.

TYPE LOCALITY. Vicinity of Gpakobo and Singrobo, southeastern Ivory Coast.

MATERIAL EXAMINED. *New records.* 1C Maize plantation, Akoto Ambiente, east of Bibiani (6°30'N. 2°08'W.), near the road from Kumasi, central Ghana; coll. J.D. Plisko, ? date; BM(NH) 1984.12.22.

OTHER RECORDS. 3C Sandy soil in Savannah between Gpakobo and Singrobo (15 km SE of Lamto, 6°13'N. 5°02'W.), southeastern Ivory Coast; (syntypes of *Millsonia lamtoiana*,Station d'Ecologie Tropicale de Lamto).

DISTRIBUTION. Southeastern Ivory Coast and central Ghana.

REMARKS. The description and the text-figures are based on Omodeo and Vaillaud (1967).

Millsonia mima (Michaelsen, 1891)

(Figs 3D & 4D)

Dichogaster mimus Michaelsen, 1891: 212; Eisen, 1900: 226; Michaelsen, 1900: 367.
Millsonia mima: Michaelsen, 1895: 31.
Millsonia mimus (sic): Omodeo, 1958: 59; Sims, 1965*a*: 299.
Millsonia rubens Beddard, 1894: 382; Beddard, 1895: 480.

DIAGNOSIS. Spermathecal pores paired in furrow 8/9, superficial by setal line *c*; combined male and prostatic pores paired on segment *xvii*, superficial, simple, located above setal line *b*; female pores paired by setal line *a* slightly anteriorly to the setal ring of *xiv*; papillae absent; clitellum extending posteriorly to *xxi* or *xxii*; 32 pairs of intestinal caeca beginning in *xxviii*; paired copulatory pouches absent; meronephric only.

DESCRIPTION. *External characters.* Length 320, 400 mm, diameter 12, 13 mm. Segments 350, 363, mainly biannulate. First dorsal pore in furrow 4/5. Clitellum *xiii–xxi*, $\frac{1}{2}$ *xxii,* saddle-shaped. Male pores combined with the prostatic pores, paired *xvii*, simple, superificial, located above setal line *b*. Female pores paired *xiv* in or adjacent to setal lines *aa*, situated about distance *ab* anteriorly to the

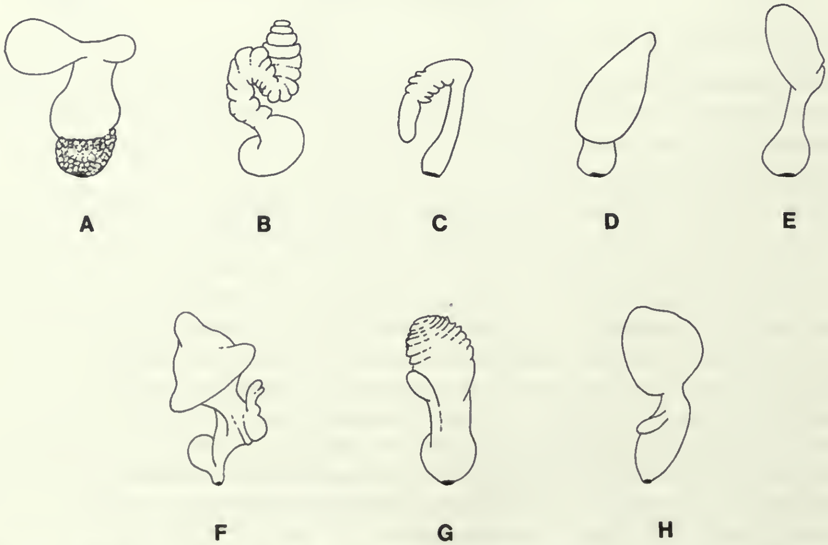

Fig. 8 Spermathecae (not to scale) of *Millsonia* spp. with spermathecal pores in furrows 7/8/9, meronephridia only present (holonephridia absent). (A)*nilesi*; (B) *pulvillaris*; (C) *guttata*; (D)*centralis*; (E)*inermis*; (F)*pumilia*; (G)*riparia*; (H)*caecifera*.

setal ring. Spermathecal pores superficial, simple paired 8/9 by setal line *c*. Papillae absent. Colour in life: pre-clitellar region violet grey, clitellum pale brown, post-clitellar region laterite (brick) red.

Setae closely paired, ventral; may be absent from the pre-clitellar region; post-clitellar formula *aa* : *ab* : *bc* : *cd* : = 6 : 1 : 4 : 1 where *dd* = three-quarters of the body circumference.

Internal characters. Septum 4/5 thickened, 5/6–8/9 delicate but 9/10 thickened with successive septa to 16/17 becoming progressively more membranous. Gizzards large, strongly muscularized. Intestinal caeca 32 pairs *xviii–lix*. Prostates single pair highly convoluted with ectally a long, coiled slender muscular portion entering the parietes in *xvii*. Single pair of spermathecae in *ix*, each with a slender ampulla leading from a stout adiverticulate duct with a verrucose basal area. Nephridia: meronephridia only present.

TYPE LOCALITY. 'Accra' Ghana. (This locality possibly denotes either the port of despatch to Europe or the address of the collector.)

MATERIAL EXAMINED. *Previously recorded*. 1C Accra, Ghana; Hungarian collection, ? date; Berlin 561 (holotype of *Dichogaster mimus*).
1C 'West Africa'; coll. A. Millson, ? date; BM(NH) 1904.10.5.546 (holotype of *Millsonia rubens*).

DISTRIBUTION. Ghana, possibly also Nigeria (? and Togo).

Millsonia moderata sp. nov.

(Figs 5D & 6D)

DIAGNOSIS. Spermathecal pores inconspicuous, paired in furrow 8/9 in setal line *a*; combined male and prostatic pores paired on segment *xvii*; female pores paired within *aa*, lying slightly anterior to the setal ring less than distance *ab* below *a*; paired spermathecal pores carried on a raised mid-ventral pad obliterating furrow 8/9 ventrally, paired small pads in the hinder region of *ix* and single mid-ventral pads present in furrows 14/15 and 15/16; setae small, usually absent anteriorly in mature individuals; eight pairs of intestinal caeca *xxvii–xxxiv*; holo- and meronephric.

DESCRIPTION. *External characters*. length 111–140 mm, diameter 5–6 mm. Segments 255–267, commonly triannulate tending towards a pentannulate condition anteriorly with the subdivision of the first and third annuli of the segments. First dorsal pore in furrow 11/12. Clitellum ($\frac{1}{2}$ *xii*) *xiii–xvi* ($\frac{1}{2}$ *xvii*), saddle-shaped. Male pores paired, combined with the prostatic pores on *xvii*, inconspicuous within setal lines *ab*; in mature individuals the mid-ventral surface of *xvii* may be invaginated to form a single copulatory pouch that, in preseved specimens, becomes evaginated and is seen as a raised glandular pad with posterior papillae. Female pores paired slightly anterior to the setal ring of *xiv* lying less than the distance *ab* below setal line *a*. Spermathecal pores inconspicuous, paired in furrow 8/9 in setal line *a*; the furrow is commonly obliterated mid-ventrally by a raised glandular trapezoidal to circular, papillose pad extending between $\frac{1}{2}$ *viii* and $\frac{1}{2}$ *xi* that carries the pores. Raised papillose pads commonly paired in the hinder region of segment *ix* by furrow 10/11 between setal lines, *cd* also a single, mid-ventral papillose pad often in each of furrows 14/15 and 15/16; other small papillose pads commonly in furrows (19/20) 20/21. Post-clitellar mid-ventral region often elevated and perhaps more heavily pigmented between setal lines *dd* chiefly over segments (*xxii*) *xxiv–xxxii* (*xxxiv*).

Setae small, closely paired and ventral; inconspicuous often absent from the pre-clitellar region. Setal formula *aa* : *ab* : *bc* : *cd* = 3 : 1·5 : 2 : 1 where *dd* is approximately one-fifth to one-quarter of the body circumference.

Internal characters. Only septum 5/6 is strongly muscular. Gizzards of equal size. Intestinal caeca, eight pairs *xxvii–xxxiv*. Prostates single pair, small, seldom extending beyond *xvii* and then only into the adjacent segments. Single pair of spermathecae in *ix*, each with a long, stout duct and bipartite ampulla; ectally the duct has a medial slender duct-like diverticulum and a lateral stouter but flattened diverticulum extending nearly to the level of the ampulla. Nephridia: meronephridia present throughout the body, also holonephridia in the intestinal region.

TYPE LOCALITY. Bozo-Akwamufie, Anom Akwam, eastern Ghana.

MATERIAL EXAMINED. 5C In the bush by the R. Volta at Boza Akwamufie, Anom Akwam, eastern Ghana; J.D. Plisko, date ?; BM(NH) 1984.4.479–483 (syntypes of *Millsonia moderata*).

DISTRIBUTION. Known only from the type locality.

Millsonia nigra Beddard, 1894

(Figs 3B & 4B)

Millsonia nigra Beddard, 1894: 384; Michaelsen, 1895: 31; Beddard, 1895: 480; Omodeo, 1958: 59; Sims, 1965*a*: 299; Sims, 1965*b*: 39; Omodeo, 1973: 17.
Dichogaster nigra: Eisen, 1900: 226; Michaelsen, 1900: 367; Cognetti, 1901: 2; Michaelsen, 1914*b*: 182.
Dichogaster eudrilina Cognetti, 1909: 1.
Millsonia eudrilina: Omodeo, 1958: 59; Sims, 1965*a*: 299.

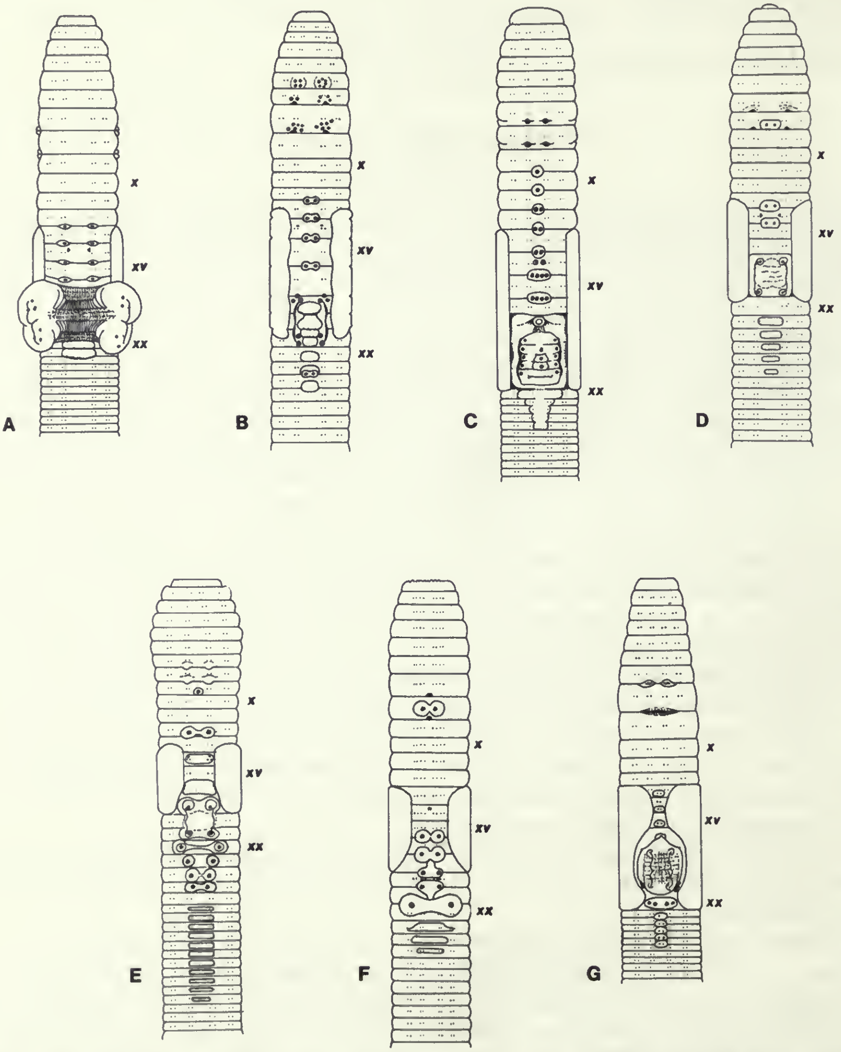

Fig. 9 *Millsonia* spp. with spermathecal pores in furrows 7/8/9, meronephridia and holonephridia present; anterior region, ventral view (not to scale). (A)*heteronephra* (male field everted); (B)*omodeoi*; (C)*ghanensis*; (D)*anomala*; (E)*brevicingulata*; (F)*ditheca*; (G)*lamtoiana*.

Diagnosis. Spermathecal pores paired in furrow 8/9 across setal lines *ab* but in adults located within a single median pouch-like vestibule; combined (paired) male and prostatic pores discharge within paired pouches with a common orifice opening *xvii*; female pores paired in the setal ring within *aa*; about distance *ab* below *a*; papillae absent; 32 (sometimes 25 to 36) pairs of intestinal caeca present; paired copulatory pouches present; meronephric only.

Description. *External character*. length 145–305 mm, diameter 13–14 mm. Segments 233–303, mainly triannulate but commonly tetrannulate in the pre-clitellar region. First dorsal pore in furrow 5/6. Clitellum $\frac{2}{3}$ *xiii–xviii*, anterior half annular but saddle-shaped by single male 'pore'. Male pores paired opening through paired copulatory pouches that discharge to the exterior through a large mid-ventral single orifice with striated glandular lips on *xvii* usually encroaching onto *xvi* and *xviii*. Female pores closely paired in the setal ring wihin *aa* located distance *ab* below *a*; they may lie in a pair of short, curving longitudinal striations or in a small, simple transverse groove. Spermathecal pores paired 8/9 across setal lines *ab* opening within a single mid–ventral pouch–like vestibule with crenulated lips that may extend between setal lines *cc*. Papillae absent.

Setae small, closely paired, ventral; post-clitellar formula $aa : ab : bc : cd = 5 : 1 : 4 : 1$ where dd = two-thirds of the body circumference.

Internal characters. Septa 4/5–13/14 strongly muscularized, 14/15 less so. Gizzards large, of equal size. Intestinal caeca usually 32, rarely 25–36, pairs beginning *xxviii*. Prostates paired, highly convoluted in the pre-caecal segments of the anterior intestine from where they lead forward to enter the parietal wall of a massive pair of copulatory pouches in *xvii* that, with full maturity, extend into *xvi* and *xviii*. Single pair of spermathecae in *ix*, adiverticulate each with a large, simple ampulla joined by a short duct to a pouch in the parietal wall that opens to the exterior by way of the vestibule in furrow 8/9. Nephridia: only meronephridia present (Beddard, 1894: 385).

Type locality. Western Province, Nigeria.

Material examined. *Previously recorded*. 1A 'West Africa' (? Nigeria); coll. A. Millson, ? date; BM(NH) 1904.10.5.535 (holotype of *Millsonia nigra*).
1C Western Province, Nigeria; coll. G.A.E. Kitson, ? date; BM(NH) 1908 11.14.1. (holotype of *Dichogaster eudrilina*).
1C Ghana; coll. C.M. Ingoldby, ? date; BM(NH) 1932.5.4.13.
1C Yaba, Nigeria; coll. A.G. Taylor, ? date; BM(NH) 1937.9.20.1.
1C Ibadan, Nigeria; coll. D.S. Madge, ? date; BM(NH) 1965.23.1.
New records. 8A Under trees around Ibadan, Nigeria; coll. D.S. Madge, ? date; BM(NH) 1970.1.779–786.
1C Zoological Gardens, University of Ife, Ile-Ife, Oyo, Nigeria; coll. A.O. Segun, ? date; BM(NH) 1978.23.17.
11C 24A Land subject to flooding by the R. Volta, Brong-Ahafo region, north Bui (8°10′N. 2°20′W.), central Ghana; coll. J.D. Plisko, 14 Sept. 1965; BM(NH) 1984.4.484–519.

Other records. 1(?) 'Olokmejd', southern Nigeria; coll. F. Silvestri, ? date; (Michaelsen, 1914*b*; 182).
1C Kumasi, Ghana; coll. J.J. Niles, ? date; (Sims, 1965*b*: 43).

Distribution. Ghana and Nigeria.

Remarks. This species forms a couplet with the mainly Ghanian species *mima*, since the immature and (?) subadult individuals of *nigra* are also large worms with paired spermathecal and male pores and both species have meronephridial excretory systems. However, the adults of *nigra* are separable externally by having a large single mid-ventral male pore and a single spermathecal vestibulum, and internally by the presence of a pair of massive copulatory pouches, while the septum of the ovarian segment is muscularized and there are usually more intestinal caeca.

Millsonia nilesi sp.nov.

(Figs 7A & 8A)

Diagnosis. Spermathecal pores paired in furrows 7/8/9 across setal lines *ab*; male pores paired *xviii*, prostatic pores paired *xvii* and *xix* within a single median copulatory pouch; female pore inconspicuous, single, mid-ventral in the setal ring on *xiv*; papillae commonly absent but occasionally on *xiv* where a raised pad extends to slightly beyond setal lines *bb* when the ventral setae may be on genital tumescences; raised, glandular areas may also develop mid-ventrally over segments $\frac{1}{2}$ *vii*-$\frac{1}{2}$ *ix* and between setal lines *aa* over segments *xxvi–xxxiii*; ventral setae slightly stouter than the lateral setae, setae closely paired; commonly 14 (sometimes 13–17) pairs of intestinal caeca (*xxvii*), *xxviii–xli*, (*xlii, xliii*); meronephric only.

DESCRIPTION. *External characters.* Length 90–182 mm, diameter 4–6 mm. Segments 142–198, mainly triannulate but further subdivision common especially in the pre-clitellar region. First dorsal pore 5/6. Clitellum *xiv–xix*, saddle-shaped. Male pores paired *xviii* (not seen externally) discharging into paired, longitudinal seminal grooves joining the (paired) prostatic pores in *xvii* and *xix*; the seminal grooves are located laterally in an invaginated genital field but, depending on the techniques employed to relax, kill, fix and preserve specimens, these may not be seen. The genital field is encircled by a raised glandular rim with an anterior and a posterior papilla, the field is invaginated with paired spherical to digitiform processes in *xvii* and *xix* usually partly lying under the external rim, other papillae may also occur. Female pore single, median ventral within the setal ring of *xiv*, usually inconspicuous but occasionally lying within a small transverse fold in the body wall. Spermathecal pores paired in furrows 7/8/9 lying across setal lines *ab*, the body-wall in their vicinity (from $\frac{1}{2}$ *vii*–$\frac{1}{2}$ *ix* between setal lines *cc*) may sometimes be slightly raised also with one or two randomly arranged papillae. Apart from these papillae and those of the male field, there are no other papillae. Sometimes the ventral surface of *xiv* may be raised between the borders of the clitellum when the ventral setae may be carried by genital tumescence, while occasionally the ventral surface on *xxvi–xxxiii* between *aa* may also be raised slightly.

Setae closely paired, small, ventral couples slightly stouter than the lateral couples; post-clitellar formula $aa : ab : bc : cd = 4 : 1 : 4 : 1$ where $dd =$ two-thirds of the body circumference.

Internal characters. Septum 4/5 thickened, 5/6–8/9 membranous, 9/10–12/13 moderately thickened. Gizzards each with a proventricular-like anterior region and a highly muscular posterior region; both large and displaced posteriorly with the hinder gizzards lying within the parietes of *ix* and *x*. Intestinal caeca, 13–17 pairs present, usually 14 pairs full-size, (*xxvii*) *xxviii–xli* (*xlii, xliii*). Prostates paired *xvii* and *xix*, each is highly convoluted with slender muscular portion ectally. Spermathecae paired *viii* and *ix*, in mature individuals the basal region of the duct has a granular appearance while distally the ampulla becomes bipartite; adiverticulate. Nephridia: only meronephridia present.

TYPE LOCALITY. Suame, near Kumasi, central Ghana.

MATERIAL EXAMINED. 1C Kordie, 16 km from Kumasi (6°50′N. 1°35′W.), central Ghana; coll. J.J. Niles, 21 Feb. 1966; BM(NH) 1968.2.80.

2C Bouhou, 13 km from Kumasi (6°50′N. 1°35′W.) central Ghana; coll.J.J. Niles, 3 Feb. 1966; BM(NH) 1968.2.78–79.

3C Agyosa village, near Kumasi (6°50′N. 1°35′W.), central Ghana; coll. J.J. Niles, 16 Jun. 1966; BM(NH) 1968.2.72–74.

1C Korofrofrom, near Kumasi (6°50′N. 1°35′W.), central Ghana; coll. J.J. Niles, 20 Feb. 1966; BM(NH) 1968.2.81.

1C Almanj, Kumasi (6°50′N. 1°35′W.), central Ghana; coll. J.J. Niles, 4 Mar. 1966; BM(NH) 1968.2.75.

1C Palm-tree plantation, University of Science and Technology, Kumasi (6°50′N. 1°35′W.), central Ghana; coll. J.J. Niles, 12 Feb. 1966; BM(NH) 1968.2.77.

1A Campus, University of Science and Technology, Kumasi (6°50′N. 1°35′W.), central Ghana; coll. J.J. Niles, Jan. 1966; BM(NH) 1968.2.76.

1C 1A Tarkwa (6°44′N. 1°40′W.), central Ghana; coll. J.J. Niles, 30 Dec. 1965; BM(NH) 1968.2.82–83.

10C 8A Suame (6°43′N. 1°36′W.), north of Kumasi, central Ghana; coll. M.A. Dawood, 12 Nov. 1966; BM(NH) 1968.2.53–71 (syntypes of *Millsonia nilesi*).

2C Bush by Kwadaso (6°42′N. 1°39′W.), central Ghana; coll. J.D. Plisko, date ? ; BM(NH) 1984.4.520–521.

1C By Lake Bosumtwe (6°30′N. 1°25′W.), central Ghana; coll. J.D. Plisko, 16 Dec. 1965; BM(NH) 1984.4.522.

2C 2A Abonn Village by Lake Bosumtwe (6°30′N. 1°25′W.), central Ghana; coll. J.J. Niles, 19 Apr. 1966; BM(NH) 1968.2.86–89.

2C Field of onions by Lake Bosumtwe (6°30′N. 1°25′W.), central Ghana; coll. J.J. Niles, 19 Apr. 1966; BM(NH) 1968.2.84–85.

DISTRIBUTION. Central Ghana.

REMARKS. The species is named in honour of Professor Joseph J. Niles of the University of the West Indies, Georgetown, Guyana, in recognition of his interest in the earthworms of the Kumasi area when he was a member of the staff at Prempeh College and later when that institution became the University of Science and Technology, Kumasi.

Millsonia nota sp. nov.

(Figs 5A & 6A)

DIAGNOSIS. Spermathecal pores in furrow 8/9 in setal line *b*; combined male and prostatic pores paired on segment *xvii*; female pores paired in the setal ring within setal lines *aa* about distance *ab* below *a*; paired papillae in furrows 10/11–13/14, mid-ventral rectangular pads in three or more successive furrows 19/20–23/24; two pairs of intestinal caeca *xxviii*, *xxix*, the anterior pair being smaller; holo- and meronephric.

DESCRIPTION. *External characters*. Length 56–72 mm, diameter 2–3 mm. Segments 179–210. First dorsal pore in furrow 8/9. Clitellum *xiii–xvii*, saddle-shaped. Male pores paired, combined with the prostatic pores on *xvii,* in *bc* about distance *ab* above *a*, located on paired porophores that are joined by a transverse ridge. Female pores paired in the setal ring on *xiv*, inconspicuous, they lie within *aa* about the distance *ab* below *a*. Spermathecal pores paired in furrow 8/9 in setal line *b*. Papillae paired in furrows 10/11/12/13/14 by setal line *b*; a single mid-ventral papilla is present in furrow 28/29 in one syntype. A transverse pad is formed from the anterior half of segment *xvi* (approaching the combined dimensions of the porophores and transverse ridge on segment *xvii*). Raised mid-ventral rectangular pads present in furrows 19/20/21/22, also perhaps 22/23/24, occupying all of the ventral surface between setal lines *bb*; each pad has a pair of slit-like transverse, pits; overall the area has a grill-like or gridiron appearance.

Setae small, closely paired, ventral; post-clitellar formula *aa* : *ab* : *bc* : *cd* = 9 : 1·5 : 5 : 1 where *dd* = two-thirds of the body circumference.

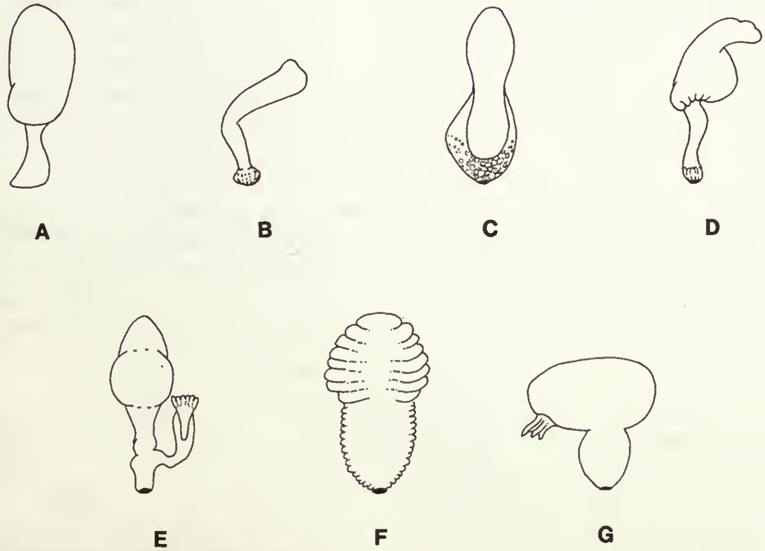

Fig. 10 Spermathecae (not to scale) of *Millsonia* spp. with spermathecal pores in furrows 7/8/9, meronephridia and holonephridia present. (A)*heteronephra*; (B)*omodeoi*; (C)*ghanensis*; (D)*anomala*; (E)*brevicingulata*; (F) *ditheca*; (G)*lamtoiana*.

Internal characters. Septa 4/5–10/11 thickened, 11/12, 12/13 less so. Gizzards strongly muscularized, of equal size. Two pairs of intestinal caeca present in *xxviii*, *xxix* with the anterior pair being small and inconspicuous. Prostates single pair, highly convoluted, lying mostly in *xviii*, ectally with a muscular duct that passes forwards into the ventral parietes of *xvii*. Spermathecae paired in *ix*, each with a long slender duct and distal ampulla, proximally there is a flattened dendritic, multilocular lateral diverticulum. Nephridia, two kinds present: meronephridia present on the parietes throughout the body and a single pair of holonephridia additionally present in each segment throughout the intestinal region.

TYPE LOCALITY. Akropong-Poana, southern Ghana.

MATERIAL EXAMINED. 2C 1A and 1A fragment (anterior region), Akropong-Poana ('New Gambia') at side of Kumasi-Dunkwas road (6°25′N. 1°40′E.), southern Ghana; coll. J.D. Plisko, date?; BM(NH) 1984.4.523–525 (syntypes of *Millsonia nota*).

DISTRIBUTION. Known only from the type locality.

Millsonia omodeoi sp. nov.

(Figs 9B & 10B)

Millsonia anomala nouvelle forme: Omodeo & Vaillaud, 1967: 929.

DIAGNOSIS. Spermathecal pores paired in furrows 7/8/9 in setal line *b*; male pores paired *xviii*, prostatic pores paired *xvii* and *xix*; female pores paired in setal line *a*; numerous small, irregularly arranged papillae form clusters posteriorly on some or all of segments *vi–viii* over setal lines *ab*, paired papillae commonly present in furrows 10/11–22/23, possibly becoming segmental behind the clitellum to segment *xxv*; seven pairs of intestinal caeca *xxvi–xxxii*; holo- and meronephric.

DESCRIPTION. *External characters.* Length 140–170 mm, diameter 4–5 mm. Segments 226–301, multiannulate. First dorsal pore 6/7. Clitellum $\frac{1}{2}$*xiii–xviii*, saddle-shaped. Male pores paired *xviii* discharging into paired seminal grooves passing between the paired prostatic pores located between setal lines *ab* in *xvii* and *xix*; paired papillae often present in the genital field. Female pores paired in setal line *a*, slightly anterior to the setal ring. Spermathecal pores paired in furrows 7/8/9 in setal line *b*. Numerous papillae are irregularly arranged in clusters over setal lines *ab* on the hinder surfaces of some or all of segments *vi*, *vii* and *viii*; paired papillae present within setal lines *aa* in furrows 10/11–22/23 often becoming segmental behind the clitellum when they may extend back as far as to segment *xxv*.

Setae stated to be the same as in *M. anomala* (i.e. small, closely paired, ventral; post-clitellar formula $aa:ab:bc:cd = 14:1{\cdot}2:9:1$ where $dd =$ three-quarters of the body circumference).

Internal characters. First septum 4/5, septa 5/6/7 greatly thickened, septa 7/8/9/10 less so. Gizzard highly muscularized in segment *vi* (no information is available on the condition of the oesophagus in segment *v*, whether the oesophageal wall is slightly thickened as in *M. anomala* was not made clear by Omodeo & Vaillaud). Intestinal caeca, seven pairs present *xxvi–xxxii*. Prostates paired *xvii* and *xix*. Spermathecae paired *viii* and *ix*, adiverticulate, very long, slenger, uniform without any differentiation into ampulla and duct (? immature). Nephridia: meronephridia occur throughout the body, additionally each post-clitellar segment contains a pair of holonephridia.

TYPE LOCALITY. Vicinity of Gpakobo and Singrobo, southeastern Ivory Coast.

RECORDS. 4C (? subadults) Sandy soil in savannah between Gpakobo and Singrobo (15 km SE of Lamto, 6°13′N. 5°02′W.), southeastern Ivory Coast; (syntypes of *Millsonia omodeoi*, Station d'Ecologie Tropicale de Lamto as *Millsonia anomala* forma *leptocystis* Omodeo & Vaillaud, 1967).

DISTRIBUTION. Southeastern Ivory Coast.

REMARKS. Omodeo & Vaillaud (1967) reported the four specimens listed above as representative of a new form of *Millsonia anomala* but I am of the opinion that, due to the magnitude of morphological divergence between this series and the seemingly sympatric types of *M. anomala*, the worms from Gpakobo/Singrobo represent a separate species. However, under Article 16 of the

International Code of Zoological Nomenclature (3rd edition 1985) a scientific name proposed with the term 'variety' or 'form' after 1960 is infrasubspecific and excluded from nomenclature, thus the epithet *leptocystis* proposed for the 'nouvelle forme' by Omodeo and Vaillaud is not an available name. It is necessary, therefore, to provide a name for this species which I do in honour of Professor P. Omodeo.

The two species *omodeoi* and *anomala* can be readily separated on their papillae patterns and, although *omodeoi* is a larger worm it possesses fewer intestinal caeca. The description and text-figure are based on Omodeo and Vaillaud (1967).

Millsonia oracapensis sp. nov.

(Figs 1A & 2A)

DIAGNOSIS. Spermathecal pores paired in furrow 7/8 in setal line *b*: combined male and prostatic pores paired on segment *xvii*; female pores paired between setal lines *a* and *b* slightly anteriorly to the setal ring; large, over 100 mm in length; anterior papillae confined to segments *vii* and *viii* and post-clitellar transverse pads present between setae *aa* on up to twelve segments; single pair of intestinal caeca *xxvii*; holo- and meronephric.

DESCRIPTION. *External characters*. Length 140–295 mm, diameter 5–6 mm. Segments 101 (? regenerating) –279; multiannulate (6–10 annuli) in the pre-clitellar region, mainly triannulate in post-clitellar region. First dorsal pore in furrow 6/7. Clitellum $\frac{1}{2}$ *xiii*–$\frac{1}{2}$ *xvii*, saddle-shaped. Male pores paired *xvii*, united with the prostatic pores in setal line *b* with associated papillae around the pore. Female pores paired *xiv* midway between setal lines *a* and *b* slightly anteriorly to the setal ring. Spermathecal pores paired 7/8 in setal line *b*. Papillae carried on segments *vii* and *viii* on a glandular area associated with the spermathecal pores; single large mid-ventral papilla usually occurs in furrow 15/16 while a pair of closely applied papillae lie within *aa* on *xix*. Raised transverse pads spread across the ventral surface between *aa* on segments (*xx*) *xxii*–*xxx* (*xxxii*).

Setae small, closely paired, ventral; post-clitellar setal formula $aa : ab : bc : cd = 6{\cdot}0 : 1{\cdot}25 : 3{\cdot}5 : 1{\cdot}0$ where *dd* approaches two-thirds the body circumference.

Internal characters. Septa 4/5–11/12 strongly thickened. Gizzards large. Single pair of intestinal caeca located in segment *xxvii*. Prostates paired in *xvii*, long and convoluted (often passing through several segments) each with a long, slender, muscular ectal region. One pair of spermathecae present in segment *viii*; each spermatheca is divided into a duct and ampulla of similar length with a multiocular diverticulum issuing from the ectal end of the duct. Nephridia of two kinds; meronephridia throughout the body with a pair of holonephridia in each intestinal segment. Internally, the external large papillae have flask-like glands.

TYPE LOCALITY. Cape Coast, Ghana.

MATERIAL EXAMINED. 1C Cape Coast, Ghana; coll. K. El-Duweini 25 Feb. 1966; BM(NH) 1968.2.26 (holotype of *Millsonia oracapensis*).
3C Cape Coast, Ghana; coll. K. El-Duweini 25 Feb. 1966; BM(NH) 1968. 2.27–29 (paratypes of *Millsonia oracapensis*).

DISTRIBUTION. Known only from the type locality.

Millsonia pulvillaris sp. nov.

(Figs 7B & 8B)

DIAGNOSIS. Spermathecal pores (paired) within deep paired vestibules in furrows 7/8/9 across setal lines *ab*; male pores paired *xviii*, prostatic pores paired *xvii* and *xix* within a single median copulatory pouch; female pores paired, inconspicuous slightly anterior to the setal ring on *xiv* lying in or slightly above setal line *a*; transverse papillose pads single or closely paired present mid-ventrally on the hinder parts of *vii*–*xvi*; setae small, closely paired; usually 14–16 pairs of intestinal caeca (*xxxvii*) *xxxviii*–*lii* (*liii*); meronephric only.

DESCRIPTION. *External characters.* Length 145–310 mm, 5–9 mm. Segments 328–410, triannulate tending towards pentannulate especially in the pre-clitellar region. First dorsal pore is located in furrow 11/12. Clitellum *xii–xix*, saddle-shaped. Male pores paired *xviii* discharge into a median copulatory pouch extending over the mid-ventrum of *xvii–xix*, also within the pouch are paired porophores in *xvii* and *xix* carrying the prostatic pores. Female pores paired in or slightly above setal line *a* of segment *xiv* where they are located a short distance anteriorly to the setal ring. Spermathecal pores paired in furrows 7/8/9 across setal lines *ab* where they are deep-set, each is located within a vestibule so that the two pairs are the same distance apart and of sufficient depth to accommodate the porophores bearing the prostatic pores. Single or closely paired papillose transverse pads extend to slightly beyond setal lines *bb* over the hinder regions of sements *vii*, *viii* (? *ix*), *x–xv*, (? *xvi*) and *xix*; the mid-ventral regions of segments *xx* and *xxi* may also be raised.

Setae closely paired, small, ventral; post-clitellar formula $aa:ab:bc:cd = 8:1:4:1$ where $dd =$ two-thirds of the body circumference; setae are commonly absent from the more anterior of the pre-clitellar segments, especially the lateral couples.

Internal characters. Septa 4/5 onwards greatly muscularized but gradually decreasing in thickness until 12/13 which is similar to the unspecialized septa of the intestinal region. Gizzards greatly muscularized with the posterior gizzard about twice the size of the anterior gizzard. Intestinal caeca, 14–16 pairs present (*xxxvii*) *xxxviii–lii* (*liii*). Prostates paired *xvii* and *xix*, highly convoluted each with a long, slender muscular ectal portion. Spermathecae paired *viii* and *ix*, digitiform although often convuluted and frequently annulated, ectally each is dilated where it enters the vestibule; adiverticulate. Nephridia: only meronephridia present.

TYPE LOCALITY. Bole, northwestern Ghana.

MATERIAL EXAMINED. 8C 4A At the roadside by a cultivated field, Catholic mission, near Bole (9°0′N. 2°30′W.), northwestern Ghana; coll. J.D. Plisko, ? date; BM(NH) 1984.4.526–537. (syntypes of *Millsonia pulvillaris*).

2C 1A Flood level by a small river, Kwunchogaw, Tuenu (10°45′N. 2°0′W.), northern Ghana; coll. J.D. Plisko, ? date; BM(NH) 1984.4.538–540.

2C Roots of a plant beside a stream, Edward Han (6°24′N. 1°32′W.), central Ghana; coll. J.D.Plisko, 25 Aug. 1965; BM(NH) 1984.4.543–544.

2C On the surface of garden soil after rain, Somanya (5°55′N. 2°55′W.), southwestern Ghana; coll. J.D. Plisko, ? date; BM(NH) 1984.4.541–542.

DISTRIBUTION. Ghana.

Millsonia pumilia Sims, 1965

(Figs 7G & 8F)

Millsonia pumilia Sims, 1965*a*: 289.

DIAGNOSIS. Spermathecal pores paired 7/8/9 in setal line *b*; male pores paired *xviii*, prostatic pores paired *xvii* and *xix*; female pores paired distance *ab* below *a* slightly anterior to the setal ring; papillae paired in setal line *b* in furrows 13/14/15/16 also a single transverse trapezoidal pad commonly present mid-ventrally over *xx* and *xxi*; ventral setae often moderately enlarged in the clitellar region, otherwise setae small and uniform; four pairs of intestinal caeca *xxvii–xxx*; meronephric only.

DESCRIPTION. *External characters.* Length 94–120 mm, diameter 1–3 mm. Segments 193–242, tetrannulate. First dorsal pore (9/10), 10/11. Clitellum *xiii–xix*, saddle-shaped extending ventrally to above setal line *b*. Male pores (not seen) open into paired seminal grooves passing between the prostatic pores discharging from paired porophores in setal line *b* on segments *xvii* and *xix*. Female pores paired slightly anteriorly to the setal ring in *xiv* located at a distance of about *ab* below setal line *a*. Spermathecal pores paired in furrows 7/8/9 occurring in setal line *a* where the adjacent body wall is frequently swollen. Paired papillae present in furrows (10/11/12) 13/14/15/16 lying in setal line *b*; a raised trapezoidal area is seen mid-ventrally across segments *xx* and *xxi* of more mature individuals, also transverse pads often present on adjacent segments.

Setae usually small, closely paired, ventral, commonly uniform but ventral clitellar setae enlarged in fully mature individuals; post-clitellar formula *aa* : *ab* : *bc* : *cd* = 6 : 1 : 4 :1 where *dd* = five-sevenths of the body circumference.

Internal characters. First septum 4/5, 4/5–10/11 stongly thickened, 11/12, 12/13 less so. Gizzards strongly muscularized, of equal size. Intestinal caeca, four pairs present *xxvii–xxx*, occasionally three or five on one side. Prostates paired *xvii* and *xix*, usually straight extending back perhaps to *xl*, or occasionally folded into one or two simple loops. Spermathecae paired *viii* and *ix*, the posterior pair being larger; duct ectally with a simple saccular diverticulum and entally with a pollux process, ampulla conical. Nephridia, only meronephridia present.

TYPE LOCALITY. Kumasi, central Ghana.

MATERIAL EXAMINED. *Previously recorded.* 5C Forest near Prempeh College (= University of Science and Technology), Kumasi, central southern Ghana; coll. M.A. Tazelaar, 21 March 1956; BM(NH) 1964.2.15–19 (holotype and paratypes of *Millsonia pumilia*).

New records. 2C Akropong Poanu (= 'New Gambia') (6°25′N. 1°40′E.), Amasie area, near the Kumasi-Dunkwa Road, central Ghana; coll. J.D. Plisko, ? date; BM(NH) 1984.4.545–546.

2 subadults 17 juvs Savanna, Wango-Fitini (near Bunkina Faso), northern Ivory Coast; coll. P. Lavelle, ? date; BM(NH) 1971.22.94–112.

DISTRIBUTION. (?) Northern Ivory Coast to central Ghana.

REMARKS. The specimens from the northern Ivory Coast, with poorly developed external characters due to immaturity, can only provisionally be assigned to this species.

Millsonia riparia sp. nov.

(Figs 7F & 8G)

DIAGNOSIS. Spermathecal pores paired in furrows 7/8/9 immediately above (adjacent to) setal line *b*; male pores paired *xviii*, prostatic pores paired *xvii* and *xix*; female pores paired distance *ab* below *a* slightly anteriorly to the setal ring; paired papillae near setal lines *b* present in furrows 14/15/16 sometimes also 10/11 with a single, mid-ventral papilla occasionally in 11/12; five or six pairs of intestinal caeca *xxvii–xxxi* (*xxxii*); meronephric only.

DESCRIPTION. *External characters*. Length 125–175 mm, diameter 4–6 mm. Segments 304–337, multiannulate but mainly tetrannulate in the post-clitellar region. First dorsal pore 7/8. Clitellum *xiii–xix*, saddle-shaped. Male pores paired *xviii* discharging into paired seminal grooves passing between the (paired) prostatic pores carried on porophores in segments *xvii* and *xix*; the mid-ventral area between the ventral borders of the clitellum in these segments being mostly smooth but depressed to form a sunken genital field. Female pores paired slightly anteriorly to the setal ring of segment *xiv*, located distance *ab* below setal line *a*; the ventral setae and the pores may be carried on a single transverse pad. Spermathecal pores located in furrows 7/8/9 adjacent to but immediately above setal line *b*, the walls of the furrows by the pores may be swollen to resemble porophores. Paired papillae are usually present in furrows 14/15/16 and sometimes in furrow 10/11 at about the same distance apart as the spermathecal pores; a single mid-ventral papilla is occasionally present in 11/12.

Setae closely paired, small, ventral; post-clitellar setal formula *aa* : *ab* : *bc* : *cd* = 6 : 1 : 4 : 1, where *dd* = two-thirds of the body circumference.

Internal characters. Septa 5/6–9/10 strongly thickened, 10/11 and 11/12 less so. Gizzards strongly muscularized and of equal size. Intestinal caeca, five sometimes six pairs present *xxvii–xxxi* (*xxxii*). Prostates paired *xvii* and *xix*, long and highly convoluted, impinging on adjacent segments; each with a slender muscular ectal region. Spermathecae paired *viii* and *ix*, each is clavate with a duct and an ampulla of about equal length; a small vestigial or incipient diverticulum may be seen laterally at the base of the ampulla of mature individuals. Nephridia: only meronephridia present.

TYPE–LOCALITY. Lake Bosumtwe area, southern central Ghana.

Material examined. 6A Campus, University of Science and Technology, Kumasi (6°50′1°35′W.), Ghana; coll. J.J. Niles; BM(NH) 1965.1.2–7.
C24 21A Various localities around Kumasi (6°50′N. 1°35′W.), Ghana; J.J. Niles; BM(NH) 1968.2.107–158.
4A Banks of the R. Wiwi (tributary of the R. Oda that flows into the R. Osin), near Kumasi (6°50′N. 1°35′W.), Ghana; coll. M. Tazelaar, 2 Mar. 1956; BM(NH) 1964.2.223–226.
1C 1A Suame (6°43′N. 1°57′W.), near Kumasi, Ghana; coll. J.J. Niles; BM(NH) 1968.2.159–160.
2C Cultivated field, Kwadaso (6°42′N. 1°39′W.), southern central Ghana; coll. J.D. Plisko, 1 Apr. 1966; BM(NH) 1984.12.6–7.
5C River bank, near Lake Bosumtwe (6°30′N. 1°25′W.), southern central Ghana; coll. J.D.Plisko, date? : BM(NH) 1984.12.1–5 (syntypes of *Millsonia riparia).*

Distribution. Southern central Ghana.

Remarks. This species is similar in size to *M. ghanensis*, and as the two species share the same damp habitat, subadult individuals can be confused. However, in addition to differences in the number of intestinal caeca, separation is made possible by the presence of indistinct traces of the paired ventral papillae in the clitellar region of *riparia* while the first dorsal pore is located more anteriorly.

Millsonia sokodeana (Michaelsen, 1912)

(Figs 3A & 4A)

Dichogaster sokodeana Michaelsen, 1912: 30.
Millsonia sokodeana: *Omodeo*, 1958: 59; Sims, 1965*a*: 299.

Diagnosis. Spermathecal pores paired in furrow 8/9 across setal lines *cd*; combined male and prostatic pores paired on segment *xvii*; female pores paired within setal lines *aa* slightly anterior to the setal ring about distance *ab* below *a*; paired papillae just above setal line *b* in furrows 15/16, 16/17, 17/18 (2 pairs), 18/19 and 19/20 while additional single, median ventral papillae are present in 16/17 and 17/18; one pair of intestinal caeca of unknown location; meronephric only.

Description. (Note. The unique holotype is dissected and incomplete, it is also in poor condition due to (past) maceration.)

External characters. Length ? (probably of only moderate length), diameter 4 mm. Segments? First dorsal pore (? 8/9), 9/10. Clitellum $\frac{1}{2}$ *xii–xix*, saddle-shaped. Male pores paired combined with the prostatic pores *xvii* in *b* in a shallow crescentic depression with a small papilla at both ends of the crescent. Female pores paired slightly anteriorly to the setal ring within *aa* at distance *ab* below *a*. Spermathecal pores paired in furrow 8/9 across setal lines *cd* each with two antero-medial papillae; pores joined by two low transverse ridges, one on each side of the furrow. Papillae paired slightly above setal line *b* in furrows 15/16, 16/17 and 17/18 (where there are an additional pair by *aa*), then 18/19 and 19/20; also a single median papilla in each of furrows 16/17 and 17/18. Raised mid-ventral rectangular pads occupy all of the ventral surface between setal lines *bb* on segments *xxvii–xxxi*.

Setae small, closely paired, ventral; post-clitellar formula $aa : ab : bc : cd = 6 : 1{\cdot}5 : 4 : 1$ where $dd =$ two-thirds of the body circumference.

Internal characters. Septa 4/5–6/7 strongly muscularized, 7/8 and 8/9 less so. Gizzards small, of equal size. Single pair of intestinal caeca, location unknown. Prostates single pair, highly convoluted in (?) several intestinal segments each with a slender muscular duct ectally entering the parietes in *xvii*. Spermathecae paired in *ix*, each with a long duct and ectal multilocular diverticulum, ampulla small entally. Only meronephridia seen in the holotype.

Material examined. 1C (subadult) Sokode, Togo; coll. F. Schroder, 1910; ZIZM, Hamburg V. 7636 (holotype of *Dichogaster sokodeana*).

Distribution. Known only from the type locality.

Notes on two new species of the genus *Agastrodrilus* (Octochaetidae) from Ghana

The genus *Agastrodrilus* was erected by Omodeo and Vaillaud (1967) to accommodate two new earthworms from the Ivory Coast that differed from species of the genus *Millsonia* in the reduced sizes of the gizzards, an increase in the length of the clitellum and the large size of the ventral setae. Subsequently, Lavelle (1981) described a third species but with a clitellum extending over only segments *xiii–xix* (like the clitella of many species of *Millsonia*), but more importantly he reported predation on other small species of earthworms. He observed one individual feeding on *Stuhlmannia porifera* (Eudrilidae) by entwining itself around the worm and swallowing it head-first, like a boa constrictor consuming its prey. His observations led him to assess the adaptive significance of the characters of the genus. The reduction in the size and weak musculature of the gizzards and the absence of a typhlosole, he interpreted as adaptations to a carnivorous diet; while the large size of the ventral setae was regarded as important in the capture and retention of the prey. These three species were described from the wet savannahs of the Ivory Coast, but specimens which prove to represent two new species have been found from the forested country of southern Ghana among material of *Millsonia* reported above.

Genus *AGASTRODRILUS* Omodeo and Vaillaud, 1967

Agastrodrilus Omodeo & Vaillaud, 1967:925.

Type species. *Agastrodrilus opisthogynus* Omodeo and Vaillaud, 1967 (new designation).

Diagnosis. Octochaetidae lacking penial setae; ventral setae (*ab*) large, at least in the pre-clitellar region; two simple rudimentary gizzards present in segments *v* and *vi*; lamellate calciferous glands paired on the oesophagus in segments *xv*, *xvi* and *xvii*; paired digitate intestinal caeca, one pair in each of several contiguous segments, present on the anterior intestine; typhlosole absent.

Distribution. Ivory Coast and southern Ghana.

Remarks. Members of this genus are remarkable not only because of their predatory behaviour but also morphologically in the case of three of the species since the locations of their reproductive systems and pores differ from those in other Octochaetidae. The two new species from Ghana described below are readily separable from the representatives of *Agastrodrilus* known from the Ivory Coast by, among other characters, the smaller number of intestinal caeca while *insolitus* sp.nov. also has the spermathecal pores situated in furrow 7/8 (see *Table 2*).

Table 2 Distinguishing characters of species of the genus *Agastrodrilus*

Prostatic pores Segment No./ Furrow	Spermathecal pores Furrow(s)	Female pores Segment No.	Intestinal caeca		Species
			No. pairs	Location	
xvii	8/9	*xiv*	8	*xxiv–xxxi*	*lavellei* sp. nov.
xvii	8/9	*xv*	19	*xlii–lx*	*opisthogynus* Omodeo & Vaillaud, 1967:926
xviii	7/8	*xiv*	5	*xxvi–xxx*	*insolitus* sp. nov.
24/25	8/9	*xxi*	24	*liv–lxxvii*	*multivesiculatus* Omodeo & Vaillaud, 1967:927
xvii + xix	7/8/9	*xiv* (by 14/15)	19	*xxii–xl*	*dominicae* Lavelle, 1981:254

Agastrodrilus insolitus sp. nov.

(Figs 11A & 12A)

Diagnosis. Spermathecal pores paired in furrow 7/8 in setal line *b*; combined male and prostatic pores paired on segment *xviii* female pores paired *xiv* within seta lines *aa*, lying in the setal ring approximately distance *ab* from *a*; paired papillae on a single, transversely oval, mid-ventral pad

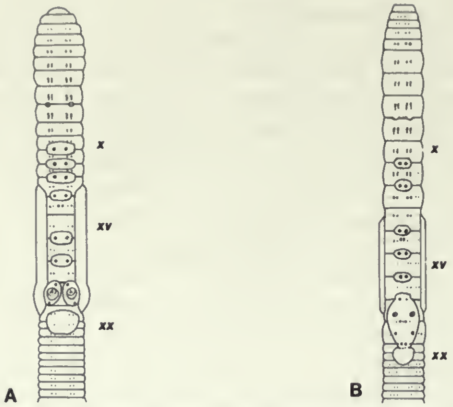

Fig. 11 *Agastrodrilus* spp. anterior region, ventral view (not to scale). (A)*insolitus*; (B)*lavellei.*

present in most furrows between the spermathecal and male pores; anteriorly setae *ab* greatly enlarged especially on segments *v*, *vi* and *vii*; five pairs of intestinal caeca *xxvi–xxx*; meronephric only.

Description. *External characters*. Length 71–110 mm, diameter 2·5–3·5 mm. Segments 126–249. First dorsal pore in furrow 9/10. Clitellum *xiii*–$\frac{1}{2}$ *xix*, saddle-shaped. Male pores paired united with the prostatic pores *xviii* slightly above setal line *b*, each located on a low porophore. Female pores paired in the setal ring of *xiv* within setal lines *aa*, each located about distance *ab* from *a* thus lying a little more than distance *ab* part. Spermathecal pores paired 7/8 in setal line *b*. Papillae paired in furrows 10/11–16/17 within *aa*, each pair on a raised oval pad extending above setal lines *b*; raised pads occasionally present within the ventral setae on segments *xx*, *xxi*.

Setae *ab* becoming progressively enlarged until long and stout on segments *v*, *vi*, *vii* and at the same time becoming more distant with the setal formula of $aa : ab : bc : cd = 5 : 4 : 7 : 1$ on *vii*, whereas setae *cd* on the same segments are small or absent; behind the clitellum setae small and uniform with the setal formula $aa : ab : bc : cd = 9 : 1 : 7 : 1$ where *dd* is three-quarters to three-fifths the body circumference.

Internal characters. Septa 4/5–9/10 strongly thickened, 10/11 and 11/12 less so. Gizzards small, weakly muscularized. Intestinal caeca five pairs *xxvi–xxx*. Prostates single pair, very long and convoluted passing through several segments, ectally becoming muscular and passing into the parietes in *xix*. Single pair of spermathecae discharging posteriorly in *vii*, each somewhat T-shaped. The duct, or lower, vertical limb of the 'T', is broad with a lateral diverticulum containing a system of branching ducts (more dendritic than racemose), while the ampulla representing the upper, horizontal portion of the 'T', has a long, main (medial) chamber and a small, subsidiary (lateral) chamber. Nephridia: meronephridia only present.

Type locality. Ada Kanyanga, southeastern Ghana.

Material examined. 18C Soil under tomato plants, Ada Kanyanga (5°55′N. 0°05′W.), S.E. Ghana; coll. J.D. Plisko, date? BM(NH) 1984.4.27–45 (syntypes of *Agastrodrilus insolitus*).
4C Cultivated field, Ada Koloidaw (5°40′N. 0°25′W.), S.E. Ghana; coll. J.D. Plisko, date? BM(NH) 1984.4.48–52.
2C By a ditch, sugar cane plantations, Kpong (6°11′N. 0°09′E.), S.E. Ghana; coll. J.D. Plisko, date? BM(NH) 1984.4.46–47.

Distribution. S.E. Ghana.

Agastrodrilus lavellei sp. nov.

(Figs 11B & 12B)

Diagnosis. Spermathecal pores paired in furrow 8/9 within setal lines *ab*; combined male and

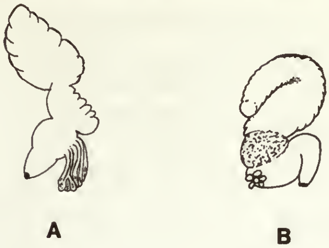

Fig. 12 Spermathecae (not to scale) of *Agastrodrilus* spp. (A)*insolitus*; (B)*lavellei.*

prostatic pores paired *xvii*; female pores paired *xiv* slightly anteriorly to the setal ring within setal lines *aa* about $\frac{1}{3}$ *aa* apart; paired papillae on a single, transversely oval, mid-ventral pad in two pre-clitellar and a further two clitellar furrows; setae *ab* greatly enlarged in the pre-clitellar region, eight pairs of intestinal caeca *xxiv–xxxi*; meronephric only.

DESCRIPTION. *External characters.* Length 80–132 mm. diameter 2·5–3·0 mm. Segments 216–289, multiannulate in the pre-clitellar segments, (up to nine annuli per segment) commonly only tri-annulate in the post-clitellar segments. First dorsal pore (9/10) 10/11. Clitellum $\frac{1}{2}$ *xiii*–$\frac{1}{2}$ *xvii*, saddle-shaped. Male pores paired on *xvii* in setal line *b*. Female pores paired on *xiv* slightly anterior to the setal ring within setal lines *aa* about $\frac{1}{3}$ *aa* apart. Spermathecal pores paired in furrow 8/9 located between setal lines *ab*. Paired papillae immediately within setal lines *aa* in furrows 10/11, 11/12, 14/15 and 15/16, each pair on a raised, transversely oval pad lying ventrally between *bb*, other papillae in the genital field (16/17, 17/18, 18/19) are similarly located nearly *aa* apart but the furrows are obliterated and an additional pair occur at *bb* on *xviii.* The genital field is usually seen as a raised scutate, glandular area, but in older individuals it may become invaginated. A further raised, glandular pad may occur ventrally between setae *bb* on segment *xx* and sometimes encroach onto the adjacent segments.

Setae in the pre-clitellar segments somewhat widely paired where *ab* are long and stout with the setal formula on segment *ix* being $aa:ab:bc:cd = 3:2:3:1$; post-clitellar setae closely paired, small and uniform, setal formula $aa:ab:bc:cd = 6:1:4:1$ where *dd* approximates to two-thirds of the body circumference.

Internal characters. Septa 4/5–10/11 strongly thickened, 11/12 and 12/13 less so. Gizzards small, weakly muscularized. Intestinal caeca eight pairs located *xxiv–xxxi.* Prostates paired, tubular, long and convoluted extending through several segments, ectally with a long, muscular duct that enters the ventral parietes in *xvii.* Single pair of spermathecae in *ix* discharge anteriorly into furrow 8/9; proximally each has a rotund, globular duct bearing a small ectal multilocular diverticulum and distally there is a wrinkled, duct-like ampulla with a diameter about one-third that of the duct. Circular, flask-like pads are present in the parietal wall internally to the external papillae. Nephridia: meronephridia only present.

TYPE LOCALITY. Near Achimota, Ghana.

MATERIAL EXAMINED. 13C Bush near Achimota, S.E. Ghana; coll. J.D. Plisko, date? ; BM(NH) 1984.4.456–467 (syntypes of *Agastrodrilus lavallei).*
4C Bush near Achimota, S.E. Ghana; coll. J.D. Plisko, date ? ; BM(NH) 1984.4.468–471.
5C 1A Green Hill, Legon, Achimota, S.E. Ghana; coll. J.D. Plisko 26 Jun 1965; BM(NH) 1984.4.473–478.
1C 'S.E. Ghana'; coll. J.D. Plisko, date ?; BM(NH) 1984.4.472.
1C Bodonya, New Achimota Village, S.E. Ghana; coll. J.J. Niles, date ?; BM(NH) 1968.2.30

DISTRIBUTION. Around Achimota (5°35′N. 0°15′E.), S.E. Ghana.

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References

Beddard, F.E. 1888. On certain points in the structure of *Urochaeta E.P. and Dichogaster* nov. gen. with further remarks on the nephridia of earthworms. *Quarterly Journal of Microscopical Science* **29:** 235–282.

—— 1894. On two new genera, comprising three new species, of earthworms from western tropical Africa. *Proceedings of the Zoological Society of London* **1894:** 379–390.

—— 1895. *A monograph of the order Oligochaeta* pp. i–vii, 1–769. Oxford: Clarendon Press.

—— 1900. On a species of earthworm from western tropical Africa, belonging to the genus *Benhamia*. *Proceedings of the Zoological Society of London* **1900:** 167–173.

Benham, W.B. 1894. On *Benhamia caecifera* n. sp., from the Gold Coast. *Quarterly Journal of Microscopical Science* (N.S.) **37:** (145) 103–112.

Cognetti de Martiis, L. 1909. Un nuovo *Dichogaster* Africano. *Bollettino del Musei di Zoologia ed Anatomia Comparata della R. Università di Torino* **24:** (599): 1–3.

Eisen, G. 1900. Researches in American Oligochaeta with especial reference to those of the Pacific coast and adjacent islands. *Proceedings of the California Academy of Sciences* Ser. 3 (Zoology) **2:** 85–276.

Gates, G.E. 1959. On a taxonomic puzzle and the classification of the earthworms. *Bulletin of the Museum of Comparative Zoology, Harvard* **121:** 229–261.

Horst, H. 1884. On two new species of the genus *Acanthodrilus* Perr. from Liberia. *Notes of the Leyden Museum* **6:** 103–107.

Lavelle, P. 1971. Recherches ecologiques dans la savane de Lamto (Côte d'Ivorie): production annuelle d'un ver de terre *Millsonia anomala* Omodeo. *La Terre et la Vie* **2–71:** 240–254.

—— 1981. Un ver de terre carnivore des savanes de la moyenne Côte d'Ivorie: *Agastrodrilus dominicae* nov. sp. (Oliogochètes–Megascolecidae). *Revue d'Ecologie et de Biologie du Sol* **18**(2): 253–258.

—— **Douhalei, N. & Sow, B.** 1974. Influence de l'humidité du sol sur la consommation et la croissance de *Millsonia anomala* (Oligochètes–Acanthodrilidae) dans la savane de Lamto (Côte-d'Ivorie). *Annales de l'Universitè d'Abidjan* Ser. E. (Ecologie) **7:** 305–314.

—— **& Meyer, J.A.** 1976. Les populations de *Millsonia anomala* (Acanthodrilidae–Oligochetes): structure, variations spatio–temporelles et production. Application d'une analyse multivariée (programme Coustel). *Revue d'Ecologie et de Biologie du Sol* **13** (4): 561–577.

Michaelsen, W. 1889. Oligochaeten des Naturhistorischen Museums in Hamburg, I. *Jahrbuch der Hamburgischen Wissenschaftlichen Anstalten, Hamburg* **6:** 1–17.

—— 1891. Terricolen der Berliner Zoologischen Sammlung. I, Afrika. *Archiv für Naturgeschichte, Berlin* **57:** 205–228.

—— 1892. Terricolen der Berliner Zoologischen Sammlung. II. *Archiv für Naturgeschichte, Berlin* **58:** 209–261.

—— 1895. Zur Kenntnis der Oligochaeten. *Abhandlungen aus dem Gebiete der Naturwissenschaften herausgegeben vom Naturwissenschaftlichen Verein in Hamburg* **13**(2): 3–37.

—— 1897. Neue und wenig bekannte afrikanische Terricolen. *Jahrbuch der Hamburgischen Wissenschaftlichen Anstalten, Hamburg* **14:** 1–71.

—— 1898. Ueber eine neue Gattung und vier neue Arten der Unterfamilie Benhamini. *Jahrbuch der Hamburgischen Wissenschaftlichen Anstalten, Hamburg* **15:** 4–16.

—— 1900. Oligochaeta. *Das Tierreich* **10:** i–xxix, 1–575.

—— 1912. Oligochäten vom tropischen und sudlich-subtropischen Afrika, I. *Zoologica, Stuttgart* **67:** 1–32.

—— 1914*a*. Oligochäten vom tropischen Afrika. *Jahrbuch der Hamburgischen Wissenschaftlichen Anstalten, Hamburg* **31:** 81–127.

—— 1914*b*. Oligochäten aus dem tropischen Westafrika gessamlt von Prof. Dr. F. Silvestri. *Bollettino del Laboratorio di Zoologia Generale e Agraria della R. Scuola Superiore d'Agricoltura, Portici* **9:** 171–185.

—— 1922. Oligochäten aus dem Rijks Museum van Natuurlijke Historie zu Leiden. *Capita Zoologica* **1**(3): 1–68.

—— 1937. On a collection of African Oligochaeta in the British Museum. *Proceedings of the Zoological Society of London* Ser. B. **107:** 501–528.

Omodeo, P. 1955. Eudrilinae e Octochaetinae della Costa d'Avorio (Oligochaeta). *Memorie del Museo Civico di Storia naturale di Verona* **4**(1954): 213–229.

—— 1958. La réserve naturelle intégrale du Mont Nimba. I, Oligochètes. *Mémoires de l'Institut Français d'Afrique noire* **53:** 9–109.

—— 1973. Oligochètes de l'Angola. *Das publicaçoes culturais da Companhia de Diamentes de Angola* **87:** 13–58.

—— **& Vaillaud, M.** 1967. Les oligochètes de la savane de Gpakobo en Côte-d'Ivoire. *Bulletin de l'Institut Français d'Afrique noire*. Ser. A. **29**(3): 925–944.

Reynolds, J.W. & Cook, D.G. 1976. *Nomenclatura Oligochaetologica: a catalogue of names, descriptions and type specimens of the Oligochaeta*. pp. i–x, 1–217. Fredericton: University of New Brunswick.

Sims, R.W. 1965*a*. Acanthodrilidae and Eudrilidae (Oligochaeta) from Ghana. *Bulletin of the British Museum (Natural History)* (Zoology) **12**(8): 285–311.

—— 1965*b*. The identity of the western African earthworm *Millsonia nigra* Beddard, 1894 (synonym *Dichogaster eudrilina* Cognetti, 1909). *Journal of the West African Science Association* **10**(1): 39–44.

Stephenson, J. 1930. *The Oligochaeta*. pp. 1–978. Oxford. Clarendon Press.

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